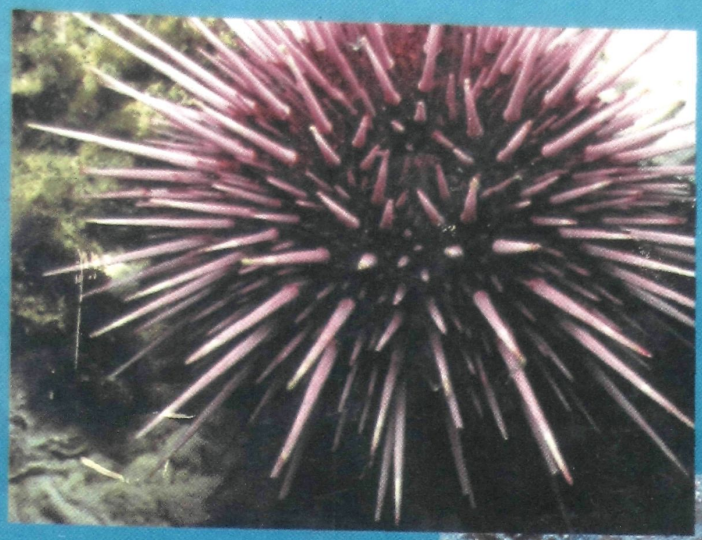

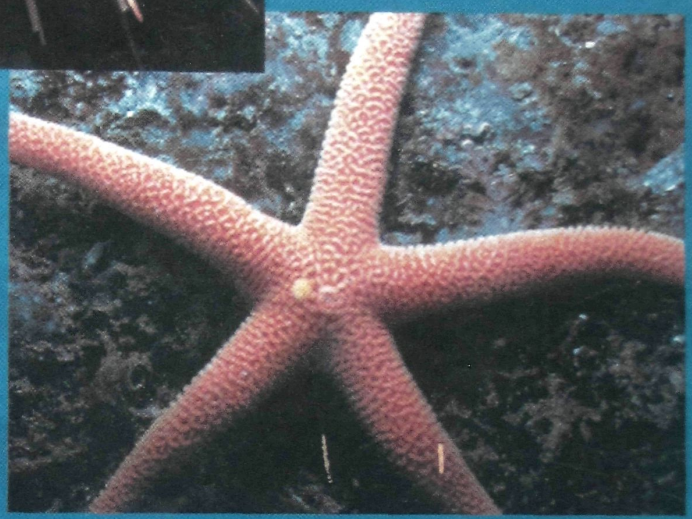

Reproductive Strategy of Marine Bivalves and Echinoderms

V.L. KASYANOV

In the Introduction to this book, the term "reproductive strategy" refers to a complex of adaptations related to reproduction. The game-theory approach to different biological events supports the correctness of this term. Larval and embryonic reproductive strategies are differentiated herein and the planktotrophic larval reproductive strategy given greater emphasis. Morphological and ecological aspects of this strategy are compared with the corresponding features of the lecithotrophic strategy.

In the first chapter, "Morphological Aspects", the larval morphology of bivalve mollusks and sea stars (as an example of echinoderms) are described and larval adaptations to pelagic environment studied. The metamorphosis of larvae and the reproduction of adults are presented with special reference to cytological features such as formation and differentiation of sex, spatial organization of gametogenesis, some gametogenic events, structure of gametes and their functioning.

In the second chapter, "Ecological Aspects", the analysis of planktotrophic strategy has focused on larval and reproductive energetics, fecundity, population, and genetic characteristics of larval and bottom semipopulations. The dependence of reproduction and the development of planktotrophic strategists on environment are emphasized. The distribution of different modes of development in various areas is described in relation to the concept of strategy.

The book concludes with a comparative table of features characteristic of planktotrophic strategy and lecithotrophic strategy and identifies new problems to be studied in future.

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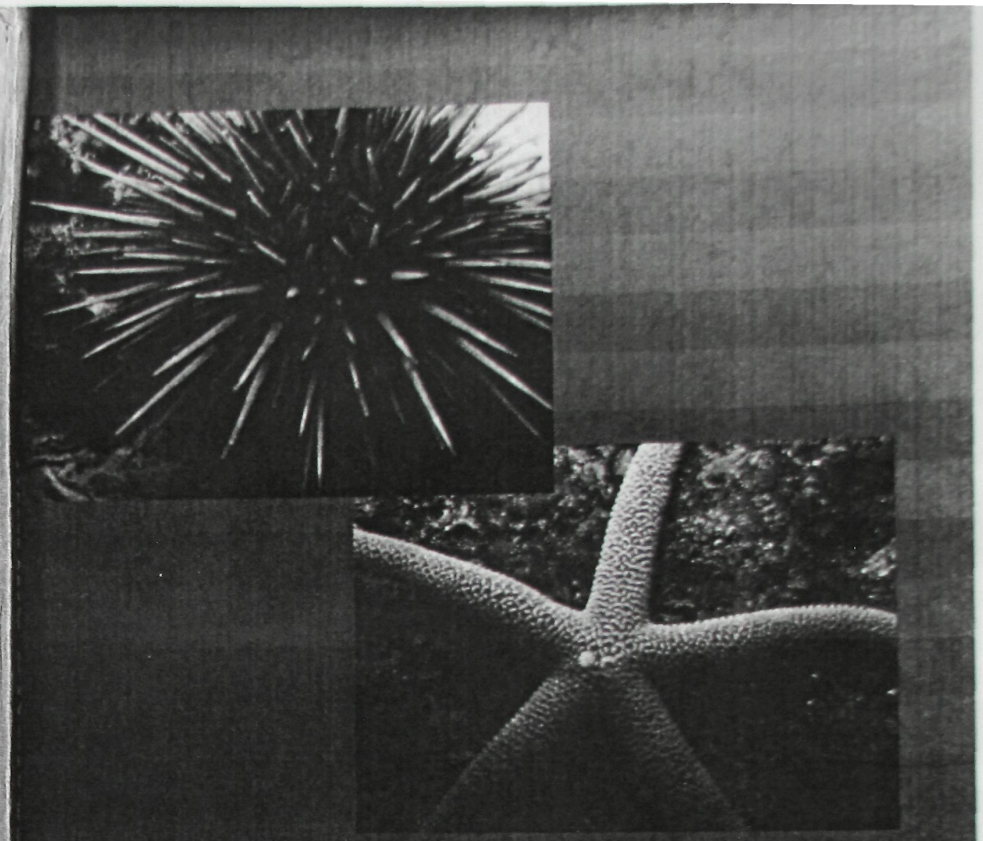

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PREFACE

To English Edition

The morphology, physiology and ecology of organisms are predominantly, and often rather exclusively, treated as the biology of adult, definitive organisms. Such an imago-centralism restricts the researcher's vision. I have attempted in this book to demonstrate that the larvae of molluscs and echinoderms constitute full-fledged organisms forming a vital and inalienable part of a population and of marine communities today as well as in the remote past. For many, as for Cameron et al. (1998), "it is a fascinating thought that in the seas of today there survives an extremely common form of embryonic development that might long predate the dawn of the Cambrian. The immediate developmental products of this basic but elegant process of embryogenesis are the marine larvae of modern, indirectly developing species. In modern forms, they serve essentially as life support systems which nourish and protect the slowly developing rudiment from which the adult body plans of their species arise".

In the decade following the publication of the Russian edition of this book, many new facts and concepts have come to light about the biology of reproduction and development of marine molluscs and echinoderms as reflected in the longer list of the literature cited, more than 500, in the present edition. This figure, of course, represents only a part of the literature dealing with the subject under study.

Although new literature has also appeared on the morphological aspects of reproduction and development, most of it contains theoretical and factual information dealing with the ecological and evolutionary-ecological aspects of reproductive strategy.

Without modifying the structural plan of the book, I have added two small sections on the cytoskeleton of gametes and reproduction in the coastal waters of oceanic islands. All other sections contain additional literary data pertaining in particular to: mechanisms of settling and metamorphosis; genetics of direct and larval development; asexual reproduction of echinoderm larvae; population genetics of marine organisms with different reproductive strategies; role of ballast water in larval transport; emergence of settled specimens in plankton and their secondary settlement; reproduction in Antarctic waters, abyssal regions

and regions of gas vents and thermal springs; and hydrological factors of transport and settlement of larvae. Referring to the latter aspect, I wish to point out that larvae, judging from their distribution in the sea, perceive it as a highly heterogeneous environment with many barriers not perceptible to human beings, but nonetheless tangible to the larvae.

October, 2000

V.L. KASYANOV

PREFACE

To Russian Edition

This book is a continuation of earlier works published by the author and his colleagues: *Reproduction in Echinoderms and Bivalve Molluscs"* (Kasyanov et al., 1980) and *Larvae of Marine Bivalves and Echinoderms* (Kasyanov et al., 1983).

The reproductive biology of bivalves and echinoderms, many of them of economic importance, is described in this work. One objective was to analyze the data on reproduction and growth that might be useful in practical aquaculture and industry and hence the scope of investigations on echinoderms has been restricted to sea cucumbers, sea urchins, and sea stars. Members of the first two classes, such as bivalves, represent objects of aquaculture and industry while sea stars damage them by attacking mollusks. This wide ranging material has been presented within a conceptual framework of types of reproductive strategy as classified by us: planktotrophic larval, lecithotrophic larval, and lecithotrophic embryonic. The book provides a detailed description of planktotrophic larval reproductive strategy and describes its consequences on the ecology, population and species features.

The book does not concern itself much with the endogenous control of reproduction of mollusks and echinoderms. The results of investigations in this sphere have been correlated in monographs by P.A. Motavkin and A.A. Varaksin (1983), the review by Lubet et. al. (1987), and in other reviews. An analysis of all the presently available theoretical models of reproductive strategy is outside the purview of this publication. I only mention the views of some and have clarified the relationship of my models with those of others but an analysis of the innumerable theoretical approaches is a task for the future.

The studies carried out for this volume were suggested and constantly supported by Acad. A.V. Zhirmunskii. The following colleagues at the Laboratory of Embryology, Institute of Marine Biology, Far East Branch, Russian Academy of Sciences, participated in the investigations as coauthors or assistants: S. Sh. Dautov, L.V. Dolgov, A.L. Drozdov, V.V. Isaeva, N.A. Kiseleva, N.K. Kolotukhina, E.S. Kornienko, G.A. Kryuchkova, V.A. Kulikova, L.A. Medvedeva, T.I. Ponurovskaya, V.N. Radashevskaya, A.A. Reunov, S.N. Yakovlev and Yu. M. Yakovlev. Collaboration with E.R.

Gaginskaya, G.V. Konovalova and V.I. Ryabushko yielded valuable data. Discussions with V.V. Isaeva, Z.S. Kaufman, O.G. Kusakin, A.I. Pudovkin and R.R. Strathmann helped me formulate my views on the problems under investigation while cordial relations with and counsel of Acad. A.V. Ivanov, L.V. Belousov, G.A. Buznikov, M.A. Gureeva, V.A. Sveshnikov, I.Kh. Sharova helped me in concluding the task satisfactorily. I utilized the facilities offered by the Biological Station 'Vostok' and launch 'Biolog' and the electron microscope center of the Institute of Marine Biology. I acknowledge my gratitude to all those who assisted me in the realisation of this book.

Biological Station 'Vostok'
Vladivostok
1985-1988

CONTENTS

And many races of living things must then have died out and been unable to beget and continue their breed. For in the case of all things which you see breathing the breath of life, either craft or courage or else speed has from the beginning of its existence protected and preserved each particular race.

-Lucretius, *"On the Nature of Things"*, I Century B.C.

INTRODUCTION

What is Reproductive Strategy ?

Reproduction is the most important function of any organism. Roughly, up to the mid-1960s, the characteristics of organisms associated with reproduction were described as the reproductive biology of species, usually without analyzing the evolutionary factors responsible for the characteristics of reproduction. During the last decade, development of the evolutionary theory and population biology has influenced the methodological approaches to describing the reproduction of organisms and the very manner of this reproduction. The biologist studying reproduction not only frequently answers the question "how?" but also attempts to answer "for what?". On the basis of the evolutionary-genetic hypotheses, assumptions were made about the evolutionary importance of phenomena associated with reproduction and variants of different reproductive methods arising in the course of the evolutionary game 'organism-environment' studied. Use of population parameters helped in quantifying the success of reproduction. Use of energetics facilitated assessment of the cost of reproduction. All of these resulted in examining reproductive phenomena in their entirety as an aggregate of adaptations ensuring the success of reproduction. Wilbur et al. (1974) termed the following as adaptive "responses" of the organism related to reproduction:

egg size, clutch size, age of sexual maturity, size of adult organism, duration of reproductive cycle, brood care, and lastly the cost of reproduction, i.e., the energy expended in reproductive activity. These and other features of reproductive strategy adopted by the organism in the evolutionary game reflect the adaptation of a species to a given habitat and the effect of selection. As pointed out by Southwood et al. (1974), the habitat of a species represents the matrix from which the pressure of selection directs it toward one or the other ecological strategy. Realization of reproductive strategy under given conditions (i.e., reproductive tactics) may change among individuals of a given population depending on its density or other factors (Nichols et al., 1976). The concept of phenotypic plasticity and reaction norm in reproduction and developmental phenomena comes close to that of "reproductive tactics" (Scharloo, 1989; Stearns, 1989). Various models have been proposed to relate the characteristics of reproductive strategy with population parameters (Giesel, 1976; Stearns, 1976, 1977, 1980, 1984; Calow, 1984; Istock, 1984).

The term "strategy" has been used in our work, as well as in several others, on analogy with its application in the game theory.

Use of the game theory terminology for describing biological phenomena has a historic background. In 1957, Waddington (1957) wrote of the need for developing the game theory to a level that would permit analysis of relationships of an organism with its environment during evolution. Lewontin's (1961) work was perhaps the first serious attempt along this line. According to him, the most interesting aspect for analysis of evolutionary problems is the class of progressively complicated games against nature. In the study of evolution of a population, Lewontin applies for this evolutionary process two possible criteria of optimum behavior of the player, viz., maximax and maximin. In the first case, the population adopts a strategy based on the extreme values of the effectiveness of moves in the game and as applicable for conditions of rapid colonization of the medium. In the second case, the population adopts a strategy in which the least value of effectiveness of a player's moves is greater than for any other strategy in all states of nature, i.e., the strategy is applicable under conditions of a saturated environment. Slobodkin (1964, p. 351) wrote: "if evolution can be regarded as a game, it is a game that can be created by Kafka or Sartre". Neither efficiency, nor complication, nor power, nor even annihilation of the opponent is per se the object of such a game; it is an awe-inspiring endless game. Its main condition is not to stop the game as this would imply death. According to Bonner (1965), the works of Lewontin and Slobodkin provide a glimmer of hope in attempts to understand the effect of diverse factors on the evolutionary process. Smith (1982) introduced the concept of stable evolutionary strategy, which has attracted the attention of evolutionists to the game theory (Rowe, 1985; and others). Chaikovskii (1965) suggested the possibility of describing

within the framework of the game theory not only micro-, but also macroevolutionary processes by treating the faunal change as a cooperative game. Later, Marchi and Hansell (1973) and Hansell and Marchi (1974) applied the game theory in reconstructing a potential evolutionary tree on the basis of the characteristics of organisms that have survived thus far. Application of the game theory concepts to biology is not confined to evolutionary problems alone. Smith (1974) analyzed the ritual conflicts between animals and Rapaport (1956) the phenomena of parasitism and symbiosis from the viewpoint of the game theoy.

Thus, concepts leading to the game theory terminology have been used time and again for analyzing biological processes. Among them is the concept of strategy by which is understood the set of moves by a player (in the present context, in the game of evolution with nature). Strategies prevailing among present-day animals and plants, viz., the strategy of reproduction, feeding, escaping from predators, etc., represent the set of adaptations that have evolved in the course of preceding games with nature. Most of the investigations on reproductive strategy have concerned land animals and plants. In the 1970s, reports were published on the reproductive strategy of marine invertebrates pointing, on the one hand, to the applicability and importance of the evolutionary-ecological approach to understanding the reproductive phenomena among marine invertebrates and, on the other, demonstrating the significant differences of their reproductive strategy from the corresponding phenomena in land animals. These differences are primarily due to the presence of larvae of marine invertebrates capable of dispersing from the parent organisms for considerable distances and later selectively settling on a suitable substrate in the course of metamorphosis. However, even the set of reproductive strategies among marine invertebrates, because of the diversity of their structures and life styles, is somewhat more wide-ranging than among land animals. It must be said that the new concepts of the reproductive biology of marine invertebrates represent only a superstructure resting on vast information that has already been collected by various investigators and correlated by Thorson (1936, 1946, 1950), Giese (1959), Shmidt (1968), Mileikovsky (1970, 1973a or b), Sveshnikov (1977) and other investigators of classical direction in the biology of reproduction and larval biology of marine invertebrates. The classic period in the development of reproductive biology of marine invertebrates can be said to have touched the zenith with the publication of the multivolume guide of Giese and Pearse (1974-1991) on the reproductive biology of marine invertebrates.

In developing the concepts on the reproductive strategy of marine invertebrates from the viewpoint of reproduction and developmental energetics, the contributions of Crisp (1974), Chia (1974), Menge (1974, 1975, 1986), Vance (1973, 1975) and Christiansen and Fenchel (1979) have been significant. The role of investigations carried out by Obrebsky (1979),

Todd and Doyle (1981), Todd (1985, from Grant and Williamson, 1985) has been considerable. According to these authors, the ecological condition of larval settling is a decisive factor in reproductive strategy. The long series of works of Strathmann (1974-1994) delving deep into nearly all aspects of reproductive strategy of echinoderms is preeminent. We shall revert to the investigations of these outstanding researchers and others in the course of our discussions. These studies are stamped with a distinct evolutionary-ecological character and push into the background the several morphological aspects of reproductive strategy. Nevertheless it is clear that any reproductive strategy is based on morphological (anatomical, histological and cytological) structures. In this book, therefore, attention is mainly devoted to the morphological aspects of reproductive biology and, on the basis of morphological data, ecological aspects of reproductive strategy are studied with due consideration of the energetics of reproductor, and evolutionary, as well as genetic constructions.

Classification of Reproductive Strategies Among Marine Bottom Invertebrates

Thorson (1946, 1950) differentiated three types of development of marine bottom invertebrates: from pelagic larva, direct development, and vivipary. Pelagic larva may be planktotrophic or lecithotrophic. While improving upon Thorson's scheme, Mileikovsky (1971, 1974) distinguished pelagic development with planktotrophic or lecithotrophic larva, demersal (bottom) development, direct development, and vivipary. Thorson as well as Mileikovsky argued in favor of a positive relationship between planktotrophic pelagic development and high fecundity of the parent stock, high larval mortality and poor stability of colonies of such species. Mileikovsky (1985) introduced the concept "pelagic larvatone" which covers the entire pelagic larvae of marine life and emphasizes the role of larvae as an effective link between all the ecological groups of marine organisms (benthos, plankton, nekton, pleuston, and neuston). Ockelmann (1965b) proposed the classification of developmental types, in particular, of marine bivalves. He distinguished: planktotrophic development characterized by small egg size and larval shell (prodissoconch I, long duration of the pelagic stage and considerable structural reorganizations during development); lecithotrophic development (eggs and prodissoconch I of moderate dimensions, pelagic stage extends for not more than a few days, larva feeds on yolk and developmental changes insignificant); and direct development (large egg size and prodissoconch I, absence of pelagic stage, feeding on yolk and frequent brooding).

Using the above classification, reproductive strategies characteristic of multicellular organisms (especially marine invertebrates) can be divided

into two groups: larval and embryonic. The former group comprises two types of strategies—planktotrophic with actively feeding planktotrophic larva and lecithotrophic with nonfeeding lecithotrophic larva. Embryonic reproductive strategies can also be divided into two variants: lecithotrophic and placental. In the first case, direct development (without larval stage) proceeds with the help of yolk accumulated during oogenesis and, in the second, with the help of a continuous supply of nutrients from the mother organism through a special organ, i.e., the placenta. These reproductive strategies form an ascending series according to the degree of intensification of the dependence of development on the mother organism: planktotrophic larval—lecithotrophic larval—lecithotrophic embryonic—placental embryonic. The exotrophic strategy, the first in this series, is distinguished by the presence of a larval digestive system and trapping organs and dependence of development on external sources of nutrients. The other strategies in this series are endotrophic, i.e., without a functioning digestive system and trapping apparatus in the larva: the embryo or larva receives nourishment in one form or the other from the mother organism. The concept of exotrophic strategy is broader than planktotrophic and is applicable to various types of actively feeding larvae, including, for example, bacteriotrophic larvae of sea stars, secondary larvae of insects, fish, and amphibians.

Among marine bivalves and echinoderms, larval exotrophy is generally planktotrophic, in subsequent discussions therefore, planktotrophic larval reproductive strategy will be analyzed. The lecithotrophic strategies—larval and embryonic—with much in common, are treated together and compared with the planktotrophic strategy. Placental reproductive strategy is not characteristic of the groups under study here and no description of it is given in this book.

In the series of reproductive strategies mentioned above, planktotrophic larval strategy occupies first place. Does this strategy represent the starting point in evolution for other reproductive strategies? Considering that the evolutionary manifestation of larvae in ontogenesis is the result of transition of ancestral forms from a holopelagic to a pelagobenthic cycle (Jägersten, 1972; Ivanova-Kazas, 1987a or b), it can be assumed that the original atrochal larvae of ancestral forms of mollusks and echinoderms were planktotrophic (or, more generally, exotrophic).

By reproductive strategy is meant exclusively sexual reproduction. The asexual reproductive strategy of bottom invertebrates is an extremely interesting but different problem (Sara, 1984). Asexual reproduction is altogether absent among bivalves and is not a frequent phenomenon among echinoderms (Ivanova-Kazas, 1977b; Emson Wilkie, 1980). Asexual reproduction by fission has been recorded for 19 species of sea star, 6 species of sea cucumber, and 34 species of brittle star; an even rarer reproduction by autotomy has been described among 7 species of sea star

(Lawrence, 1987). A detailed description and analysis of the importance of asexual reproduction in echinoderms from the viewpoint of reproductive biology have been given by Mladenov et al. (1983, 1986), Mladenov and Emson (1984) and Mladenov and Burke (1994). Only four types of sea stars with apparently inconsistent properties have been detected: these produce planktotrophic larva but concomitantly their fecundity is very low at 200 to 500 eggs. These sea stars—*Linckia multiflora*, *Ophidiaster robillardi*, *Sclerasterias richardi* and *Nepanthia belcheri*—usually reproduce asexually (Ottesen and Lucas, 1982). Populations of sea stars *Stephanasterias albula* and *Asterina burtoni* reproducing exclusively asexually were recently reported. Further, the absence of rudiments of a sexual system and related aboral hemal and perihemal rings have been demonstrated histologically in *S. albula* (James, Pearse, 1969; Mladenov et al., 1986). Finally, a sea star with exclusively parthenogenic reproduction has been detected: populations of females of *Ophidiaster granifer* and larvae growing from them represent the only known example to date of natural parthenogenesis among echinoderms (Yamaguchi, Lucas, 1984). The evolution of parthenogenesis, rare in mollusks and echinoderms, is restricted by limitations imposed by development. These limitations may be cytological and genetic as a result of differences in ploidy and concentration of mutations or reduction of heterozygosity (Kondrashov, 1997, 1998). Rejection of sexual reproduction and transition to asexual reproduction in sea stars (as in other animals for which asexual reproduction is characteristic) may be at the level of individual populations or colonies of a single species. On the western Australian coast, recruitment of populations of sea star *Coscinasterias calamaria* is essentially by asexual reproduction and not from a larval pool as in other regions (Johnson, Threlfall, 1987). On the Mediterranean coast of Israel, sea star *Asterina burtoni* reproduces only asexually notwithstanding the presence of testes with a spermatogenic cycle; this star on the Red Sea coast reproduces by the common sexual method as well (Achituv, Sher, 1991). In fact, populations of *Coscinasterias calamaria* reproducing by division on the coast of New Zealand contain only males (Crump, Barker, 1985).

In brittle stars *Ophiocomella ophiactoides* and *Ophiactis savignyi*, settlements in algal undergrowths are represented by clones formed through asexual reproduction (Mladenov, Emson, 1988, 1990). Asexual settlements of *Ophiactis savignyi* in sponges are also represented predominantly by males (Mladenov, Emson, 1988). Various explanations are possible for the absence of females in asexual populations of echinoderms. According to one explanation, species with asexual populations represent protandrous hermaphrodites and asexual reproduction commencing in the protandrous phase prevents reversion to the female phase. Another explanation is that asexual settlements originated from males that were more successful than females in surviving

adverse conditions (Achituv, Sher, 1991). Finally, the shift of sex ratios in favor of males reduces the energy consumption in germ cell production by enhancing the possible frequency of fission of individuals (Chao, Tsai, 1995).

Judging from the population and genetic data, sexual as well as asexual reproduction occurs in brittle star *Ophiomyxa brevirema* on the coast of New Zealand with direct development. A combination of the two reproductive methods broadens the reproductive success of this species (Garrett et al., 1997). In some populations of sea cucumber *Holothuria atra*, asexual reproduction is the main method of sustaining the population level (Chao et al., 1994). Among sea cucumbers *H. atra* and *H. edulis* from the Great Barrier Reef, sexual and asexual reproductive cycles have not been correlated and mature individuals reproducing asexually may be found (Uthicke, 1997).

It was recently found that asexual reproduction of sea stars is possible even in the larval stage. This is an enigmatic phenomenon of interest from the embryological point of view compelling us to consider the balance of favorable and adverse consequences of such a phenomenon for sea star populations (Jaeckle, 1994; Jaeckle, Bosch, 1995). Several variants of morphogenesis during asexual reproduction of bipinnaria accompanied by processes akin to gastrulation have been detected (Jaeckle, 1994).

Another paradox that requires more detailed analysis is the asexual reproduction of brittle star larvae (Balser, 1996). Asexual reproduction of larvae of brittle star *Ophiopholis aculeata* and of another unidentified species of brittle star commences with the detachment of posterolateral arms from the pluteus of the brittle star. These arms regenerate the entire structure of the new larva by reorganizing their tissues. Secondary larvae of *O. aculeata* undergo metamorphosis, settle and give rise to the third generation of larvae, once again by detachment of arms. This procedure thus offers an unusual potential for enlarging the distribution range and population of juveniles (Balser, 1998). According to observations of Balser (1998), during asexual reproduction of brittle star larvae, a blastocoel-like structure is formed and gastrulation proceeds followed by formation of larval intestine, coeloms, and other larval organs.

All these examples are interesting not just because of their unusual characteristics, but because they broaden out knowledge of reproductive methods in sea stars brittle star and echinoderms in general. An analysis of these examples will help us later in coming even closer to understanding the role of larvae and the importance of the sexual process in the reproduction of marine invertebrates. Attempts of Mladenov et al. (1983, 1986) to apply theoretical models of evolutionary advantages of the sexual process to an analysis of sexual and asexual reproduction among echinoderms and its rejection (Bell, 1982) are encouraging. Theoretically, a combination of sexual and asexual reproduction would be an ideal

strategy as it would draw the best from each type of reproduction (Corley et al., 1999; Corley, Moore, 1999).

Reproductive strategy often (but not invariably) determines the form of strategy of the entire life cycle or, in other words, the life pattern of a species, according to Beklemishev (1970; see also Sharova, Sveshnikov, 1988). Reproduction is not the only game that an organism plays with the environment. Along with reproductive strategy, the organism adopts in its life certain strategies for development, acquiring food, escaping predators, socialization and exploitation of space. These distinct strategies constitute the overall strategy of the life cycle, for examle, r- or K-strategy, strategy of opportunistic species or specialist species; competing and tolerant strategies and evasive strategy typical of violent, patient or "explerent" (after L.G. Ramenskii) species and others (Ramenskii, 1935; Whittaker, Goodman, 1979; Stearns, 1980, 1984; Wilbur, 1980; Pianka, 1981; Hornbach et al., 1982; Sveshnikov, 1983; Bayne, 1984), In this context, let us expound on the relationships between planktotrophic and lecithotrophic reproductive strategies with r- and K-strategies.

MacArthur, Wilson (1967) distinguished two types of effects of natural selection on a population: r-selection acting when resources are available for enlarging the population strength and K-selection acting when the medium has reached maximum density. r-selection promotes accumulation of such characteristics in a population as will ensure its rapid growth under conditions of an ecological vacuum while K-selection promotes accumulation of characteristics that ensure the stability of the population under conditions of fullness of ecological niches. Following a study of the effect of r- and K-selection, MacArthur and Wilson analyzed the changes occurring within the life of a given population. These changes may affect the fecundity of individuals, intensity and duration of spawning, and other parameters which are readily influenced by environmental factors, i.e., parameters of a tactical nature.

Along with r- and K-selection concepts, r- and K-strategy concepts are extensively used (see, e.g., Pianka, 1981). How are the planktotrophic and lecithotrophic strategies under consideration related to r- and K-strategies? Firstly, r- and K-strategies describe the life cycle of the population as a whole while planktotrophic and lecithotrophic strategies represent distinct events of strategies of the life cycle, reflecting adaptation associated with reproduction. Secondly, r- and K-strategies combine adaptation of the entire population and to some extent of the species, but not of individuals; reproductive strategies represent the aggregate of morphological adaptations to reproduction characterizing primarily the individual organism. Thirdly, the concept of r- and K-strategies arose from an analysis of quick responses of a population to environmental changes and is essentially applicable to those very specific situations; reproductive strategies based on the complex of morphological characteristics describe

differences on a macroevolutionary scale. Therefore, a given species with planktotrophic or lecithotrophic strategy may at different times fall under the influence or r- or K-selection shifting along an r-K continuum in any direction. Under conditions of a brief effect of r-selection, the fecundity of one or the other species may rise while, under conditions of K-selection, it may fall without, however, affecting the pattern of development.

Some successors of MacArthur's approach to population evolution and dynamic biogeography (MacArthur, 1972) extend the concept of r- and K-selection to macroevolutionary processes. In such an approach, under conditions of prolonged effect of r-selection, a set of adaptations characterized by planktotrophic reproductive strategy will evolve while, under conditions of a prolonged effect of K-selection, a lecithotrophic reproductive strategy will arise.

However, when studying the simplified model of r- and K-selection, one should not forget that "the constant repetition of the same hypotheses in literature may give the impression that a satisfactory explanation exists already or that the explanation would be simple" (Strathmann, Strathmann, 1982, p. 91). The r- and K-models of selection have undergone extremely severe criticism for a loose definition of the concept of the capacity of the environment, for oversimplification of the factors of selection, and for other deficiencies (Wilbur et al., 1974; Stearns, 1977; Whittaker, Goodman, 1979; Bergmans, 1984). Nevertheless, the simplicity and clarity of concepts of r- and K-models render them convenient for a comparative analysis of the dynamics of various populations.

The boundary between planktotrophic and lecithotrophic strategies is not the state geographical demarcation and lecithotrophy (some amount of yolk is present in the eggs of all animals) is noticed in the early larval life even among planktotrophic organisms. Within the planktotrophic strategy, the extent of its manifestation differs among different species and one could conceive a continuum of species with planktotrophic and lecithotrophic strategies. A given species (even the same population) may adopt, although rarely, planktotrophic as well as lecithotrophic strategies. Such exclusive examples have been noted before in polychaetes and gastropods but information is now available about the combination of both the strategies even in bivalve mollusks. Booth (1979) was the first to propose for brooding *Kellia cycladiformis* and later Cranfield and Michael (1989) demonstrated in brooding *Tiostrea chilensis* that these mollusks could discharge larvae not immediately before settling as is usual, but somewhat earlier, necessitating their prolonged residence in plankton. The consequences of such behavior in females for the settlement of the species and for genetic exchange between populations are undoubtedly significant but their causes are not known.

In fact, a combination of brooding and active feeding is possible. Thus, endoscopic observations showed that larvae of brooding oyster *Ostrea*

chilensis are capable of active feeding by circulating in the mantle cavity of females (Chaparro et al., 1993).

The aspects of reproductive strategy, like any other life strategy, are indeed diverse. These may be morphological, physiological, behavioral, biochemical and so on. The selection of one or the other reproductive strategy in the course of evolution involves certain consequences. Dynamics of population, its age composition, and sex ratio fall under the influence of reproductive strategy. It is reflected in such characteristics of a species as its distribution range and duration of life cycle.

The concept "supply side" ecology (Lewin, 1986; Underwood, Fairweather, 1989) conceived in the 1980s emphasizes the important role of food availability for the larvae in determining the ultimate structure of benthic communities (Arnold et al., 1998). In particular, the leading role of recruitment by larvae or juveniles is regarded as a key factor controlling some shallow-water communities on hard grounds (Roughgarden et al., 1994). In the case of communities on soft grounds, however, processes occurring with the larvae before settling are less important than postsettlement processes (Olaffson et al., 1994). In fact, the modal experiments of Young et al. (1998) point to the leading role of factors controlling larval inflow even in the subsequent formation of these communities.

Having attempted a description of planktotrophic and lecithotrophic strategies, it is my opinion that morphological (anatomical, histological and cytological) features characteristic of an organism should be regarded as dominant traits. Individual organisms and not the population or species represent the object of natural selection (Williams, 1966); individual organisms, however, are characterized primarily by morphological features possessing fairly conservative as well as potentially variable characteristics so as to form a base for diverse adaptations of the organism, including adaptation for reproduction. Morphological conservatism and constraints of structural plan of the organism channelize the evolutionary development of reproductive strategy within the large taxa of animals or plants and serve as a "morphological imperative" of the strategy (Stearns, 1977, 1984; Bergmans, 1984). In those cases wherein a migration of organisms into new habitats in the course of evolution has taken place, conservatism of reproductive strategy compels many animals to return to their former habitat to reproduce: thus, sea turtles lumber on shore for oviposition while the female robber crab enters the sea for spawning.

MORPHOLOGICAL ASPECTS

In the introduction to the proceedings of the symposium on evolutionary morphology of marine invertebrate larvae, Emlet and Ruppert (1994) recalled with regret Williamson's (1992) words: "It is said time and again that morphological investigation of invertebrates is old hat." Yes, but what a cache of secrets the hat conceals!

Planktotrophic Larvae

Planktotrophic larvae of marine invertebrates constitute a significant component of pelagic coastal waters. In their developmental stages, they simultaneously "resolve" immediate problems of nutrition, distribution, escape from predators and competitors, etc. The larvae are very similar in morphology, physiology, and behavior irrespective of differences in ecological niches inhabited by adults. Such a similarity is the result of adaptation to a pelagic life style. Contrary to the diversity of ecological conditions in the period of their demersal life cycle, organisms in the water column encounter a more homogeneous environment. Larvae of marine bivalves and echinoderms may be considered entirely free-living organisms equipped with all the systems of organs for habitation in pelagic zones. Although larval structure and functions have been described before (Kasyanov et al., 1983, 1998; Kasyanov, 1984 a, b), it would be advantageous to present the material in this context with some additional information describing the features of the decisive element of planktotrophic reproductive strategy. Larvae of sea stars serve as an example of larvae of echinoderms.

Veliger and Bipinnaria

Feeding

Capture of food and its transfer to the oral opening in veligers of bivalves is accomplished by the ciliated bands of the velum. Cragg (1989) has detailed the structure of the ciliated bands in *Pecten maximus*. Food particles from the long cilia of the preoral band are passed to the adoral band at the level of the oral opening. The distance between these bands in the

veliger of *Ostrea edulis* is several microns: the length of cilia of the adoral band is about 8 μm and the width about 20 μm. Food particles are encased in mucus as they move along the adoral band toward the oral opening. Below the adoral band, under the oral opening, there is a postoral ciliated band consisting of a single row of complex 15-20 μm long cilia. The coordinated beating of cilia of pre- and postoral ciliated bands ensures, according to Strathmann et al. (1972), the concentration of food particles captured from water by the ciliated bands. The more the cilia in the preoral band, the greater the rate (and lower the efficiency) of particle filtration (Strathmann, Leise, 1979). In seizing food particles, the preoral as well as postoral ciliated bands participate with the cilia beating in opposite directions (Strathmann, 1987). Larvae of *Mercenaria mercenaria* capture particles as they traverse through the restricted zone of the ciliated band above the return wave of preoral cilia (Gallager, 1988). The research technique adopted by Emlet (1990a) revealed that preoral cilia of the larvae of *Crassostrea gigas* measuring about 90 μm in length beat at an angular rate of 150 rad s^{-1} and cause the advance of particles in the velum region at 6-7 mm s^{-1}; further, in the absence of flow through a 1 μm long ciliated band section, water traverses at about 2 mm^3 s^{-1}.

The postoral tuft of cilia formed by the postoral ciliated band lies in the buccal region. According to Waller (1981), these cilia may perform a sensory function or facilitate expulsion of excess mucus or excess food from the mouth.

The oral opening situated at the edge of the lower part of the velum leads to the esophagus. Cells of the latter contain vacuoles and bear powerful cilia that fill the esophageal lumen and project through the oral opening. The stomach comes next in the digestive tract. The digestive gland looks like two pouches (lobes) arising from the stomach. The cells of this gland are very large and sometimes greenish or reddish-brown depending on the food ingested. Accumulated granules of food matter are visible in them (Meisenheimer, 1901). Neutral lipids, and not glycogen as in adult mollusks, comprise the principal energy reserve of larvae (Holland, Spencer, 1973; Holland, 1978). A changeover to new reserve nutrients takes place in 3- to 5-month-old spat (Holland, Hennant, 1974).

The gland of the crystalline style, formed on the right side of the posterior part of the stomach, is lined with cilia. At the end of larval life or after the larva settles to the bottom, cells of this gland secrete the crystalline style containing digestive enzymes. Microalgae containing unsaturated fatty acids are essential for normal larval development of bivalve mollusks. New enzyme systems, some facilitating the synthesis of unsaturated fatty acids, are seen in juveniles (Robert, Trintignac, 1997). Behind the stomach is the small intestine which forms a loop and in larvae of *M. edulis*, the cecum (Bayne, 1971). The gut epithelium is simple, flattened, and bears cilia. The small intestine passes into the

short hindgut (proctodeum) with vacuolated cells. The proctodeum opens exteriorly through the anus; cilia are visible in its lumen.

The gut wall lacks muscles and food movement through it is evidently accomplished by cilia. In larvae of some species, there is a postanal tuft of dense 15 μm long cilia behind the anal opening which is surrounded by short cilia. The postanal tuft facilitates excretion of fecal matter from the mantle cavity.

The digestive system of sea star larvae—bipinnariae—comprises the mouth cavity, esophagus, stomach, and a short thin intestine terminating in the anal opening. Larvae of sea stars and other echinoderms feed on food particles suspended in the ambient water. Feeding of such organisms involves generating a water current, separating food particles from the water, transporting them to the mouth, and ingestion.

Evidently, larvae of sea stars do not possess chemoreceptors for discerning the quality of food ingested since they ingest not only unicellular algae, but also coal particles (Dautov, 1979). The perioral depression or the oral field participates in food capture but the main trapping apparatus comprises three ciliated bands; the small preoral band, postoral band edging the entire body (except the preoral plate), and adoral band bordering the oral opening. The preoral band passes into a medioventral and two preoral projections while the postoral band passes into the mediodorsal and paired postoral, posterolateral, posterodorsal, and anterodorsal projections. In bipinnariae, projections bearing the ciliated bands are supported by a gel filling the extensive cavity of the larval body (Strathmann, 1989). The degree of development of any projection is considered when defining the species affinity of a larva. In some species of sea stars, the ciliated band is barely discernible on the projections (members of genera *Asterias*, *Pisaster*, and *Pycnopodia*) while it is distinctly manifest in others (*Patiria* and *Luidia*) (Strathmann, 1971). The ciliated band attains maximum length in the bipinnariae of *Luidia* (Meek, 1927, cited from Strathmann, 1971; Wilson, 1978). The adoral band forms two strands passing along the ventral side of the esophagus to form a long stretched loop. In larvae of sea stars, the entire outer surface of the body is armed with individual cilia.

The cilia in the various bands range from 20 to 30 μm in length. Each band is about ten cells wide and each cell bears one cilium. Cilia beating at a right angle to the ciliated band generate the main water current which advances the larva. At the time of larval feeding, food particles are trapped on the ciliated band and later transported by the band and cilia of the perioral field to the mouth.

According to Strathmann (1971), the mechanism of movement of particles by the ciliated band is presumably as follows: particles of adequate size which come into contact with cilia of the band during active beating (directed from the perioral field) mechanically or chemically

induce a local temporary reversal of beating of contact cilia. As a result of reversed beating, trapped particles are transported to the perioral field and then to the mouth. Once these particles are delivered into the perioral field, the initial direction of active ciliary beating is resumed. The captured particles enter the oral cavity through the upper and lateral sections of the adoral band. Cilia of these areas, like those of the esophageal loop of the band, beat in the direction of the intestine. Particle advancement to the mouth is evidently facilitated by the secretion of mucous cells located alongside the ciliated band. Food particles entering the mouth cavity may remain there for over 20 min, during which time they congeal into a compact mass. Some particles enter the esophagus without being detained (Strathmann, 1975a). Coal particles added to the culture of bipinnariae of *Aphelasterias japonica* were detected in the esophagus after 50-60 s and in the stomach 2 min later (Dautov, 1979). Analysis of a video recording of particle seizure by the ciliated band of bipinnariae (Hart, 1991) confirmed Strathmann's conclusions regarding the mechanism of concentration of food particles in the ciliated band in bipinnariae and other larvae of echinoderms and contradicts the conclusions of Gilmour (1988a, b). Gilmour's postulation of particle seizure by cilia of the perioral field bypassing the ciliated band is possible but cannot be considered the main method of food seizure. Ciliary reverse beating which concentrates food particles in the ciliated band is suppressed in the absence of calcium ions (Hart, 1990).

All sections of the digestive tract are lined with ciliary cells that assist in the passage of food particles. Oblong and circular esophageal muscles assist in the passage of food particles through the esophagus. The pulsating contractions of these muscles push the food forward into the stomach, which is separated from the esophagus by the cardial sphincter. Food enters the small intestine through the open pyloric sphincter. Particles are sorted into digestible and nondigestible in the stomach. Passage of food particles through the entire digestive system takes 15 to 20 min.

Respiration

There is no specialized respiratory apparatus in larvae of bivalves. Oxygen inhalation and carbon dioxide exhalation proceed through diffusion. Since diffusion is facilitated by water flow, various locomotory hydrokinetic structures of larvae, in addition to other functions, also accomplish respiration. These structures include primarily the pre- and postoral ciliated bands as well as the ciliated tracts of the esophagus and gut. Respiration is possibly assisted further by cilia situated along the margin of the mantle cavity, including the region of future gill formation.

As in larvae of bivalves, the intake of oxygen and removal of carbon dioxide in larvae of sea stars occurs by diffusion. The minute size of

larvae enables them to dispense with a specialized respiratory system. Their constant motion, beating of ciliated bands and cilia of other areas of the body surface, as well as the ciliated surface of the digestive system promote gaseous exchange of larval tissues with water.

Transport of substances

There is no circulatory system in larvae of bivalves. The transport of substances, especially nutrients, from the digestive system to other parts of the body occurs through the extensive body cavity. Transport of various substances in the cavities is accomplished by muscular contractions and relaxations in the veliger. The body cavity of larvae of *Crassostrea virginica* and *C. gigas* contains phagocytes (similar to those of definitive individuals) participating in the processes of excretion as well as coelomocytes not involved in phagocytic processing but which evidently process and transport dissolved nutrients secreted by cells of the digestive system (Elston, 1980).

In echinoderm larvae too, likewise of minute dimensions, there is no need for a special blood circulatory system. This function is fulfilled by the extensive primary and secondary body cavities. Transport of substances in the primary body cavity is facilitated by muscular contractions of the body wall and esophagus while the transport of substances in the secondary cavity (coelom) is facilitated additionally by the beating of cilia lining the coelomic cavities.

Excretion

In the larvae of some bivalves, unlike those of other mollusks (except for pulmonate gastropods), the excretory system is represented by larval protonephridia. These have been described for *Dreissena polymorpha, Teredo navalis, Ostrea edulis,* and *Codakia orbicularis* (Hatschek, 1880; Meisenheimer, 1901; Waller, 1981; Alatalo et al., 1984). Protonephridia originate from the ectoderm and are arranged on both sides of the body, under the epithelium, extending from the esophagus to the base of the foot. A protonephridium consists of two or three cells. The ciliary cell often contains a vacuole and has a tuft of very long cilia in the protonephridial canal that extends up to the excretory pore. The canal is formed by the second cell. The third cell delimits the excretory pore of the protonephridium. Protonephri-dial pores lie deep in the mantle cavity.

Protonephridia have not been detected in veligers of other mollusks—*Pandora inequivalvis, Cerastoderma edule* (Creek, 1960; Allen, 1961), and others. Possibly the excretory function is performed by coelomocytes diffused throughout the body cavity. Elston (1980) has described the passage of coelomocytes loaded with spent substances from the body cavity through the velar tissue into the mantle cavity.

Larvae of sea stars have no specialized excretory system. As in many lower groups of animals, the excretory function is undertaken by the developed digestive system. Evidently, mesenchymal cells dispersed in the primary body cavity participate in the removal of metabolic products. Field (1892) may be correct since his demonstration of the excretory function of the pore canal was partly confirmed by the organized directional movement of cilia in the coelomic cavities (Gemmill, 1914) which generates fluid flow toward the pore canal. Ruppert and Balser (1986) are more specific in naming the canal-hydropore complex the nephridium.

In the course of development of sea stars, coelomic structures undergo very significant transformations. They form various organs and systems in the definitive organism, primarily its ambulacral system. In describing coelomic formations of bipinnariae, they are treated as multifunctional structures performing supportive, distributive and excretory functions.

Coeloms of bipinariae are in the form of extensive hollow pouches dispersed on both sides of the digestive tract. In the early bipinnariae, they are separated above the oral lobe but are later joined before transiting into the dorsomedial projection. The left side of the coelom is better developed than the right. Septa in the posterior region of the coelom partly separate the left and right somatocoels from the common coelom. This separation becomes complete later. The rest of the coelom is a single structure that later separates into left and right, anterior and median coeloms, i.e., axo- and hydrocoels. This single coelom is linked with the external medium through a pore canal which opens as a hydropore on the dorsal side left of the median line at the level of the lower part of the esophagus. In some species, in addition to the left pore canal, there may be a right pore canal which also opens through a hydropore exteriorly (Field, 1892; Gemmill, 1914, 1915). During bipinnarial development, coeloms of the right and left sides fuse not only in the anterior region, but also in the region of somatocoels. The left somatocoel forms a temporary process, termed the ventral horn, which comes into contact with the right axocoel ventral to the stomach and encircles the intenstine from the both sides. A dorsal horn also forms in the left somatocoel and establishes contact with the left axohydrocoel. Thus, coeloms of the left side remain connected despite a dividing septum.

According to Gemmill (1914), the flow of coelomic fluid is directed by cilia from the left axohydrocoel to the right axohydrocoel through the preoral cavity and from there through the ventral horn to the left somatocoel and again into the left axohydrocoel. In the pore canal lined with cuboidal ciliated epithelium, as mentioned above, a weak outward beating of cilia is perceived. Possibly, fluid movement in the coelomic cavities is promoted by pulsation of the closed madreporic vesicle (formed in all probability from mesenchymal cells) situated alongside the left

hydropore (Gemmill, 1914). This vesicle has not been detected in all species, nor do all authors mention the circulation of coelomic fluid (see, for example, Barker, 1978a).

Locomotion

In the veliger, swimming consists of vertical rise followed by descent. The veliger moves in water by ciliary beating of the ciliated ring along the rim of the velum. The velum in bivalve larvae is usually oval. A remarkably large bilobate velum is found in transoceanic and deepwater species. Such is the velum of the transoceanic larval of *Planktomya henseni* belonging to a hitherto unidentified species (Allen, Scheltema, 1972). Larvae of teleplanic tropical pinnids (Scheltema, Scheltema, 1984; Scheltema, 1998) have a large bilobate velum similar to that in the larvae of gastropod mollusks. A larger velum facilitates larval migration to long distances and efficient collection of food particles (scarcer in open seas) since an increase in velum size means an increase in number of ciliated rings. For example, in deepwater pholadid *Xylophaga atlantica*, the larva has no less than six rings (Culliney, Turner, 1976).

Beating of the cilia produces an upward and somewhat forward movement of the veliger during which the velum is slightly inclined forward relative to the axis of movement. The posture of a swimming veliger resembles that of a helicopter in flight. The principal locomotory organ is the outer preoral ciliated rim of the velum consisting of a double row of ciliaciliary cells. In the veliger of *Ostrea edulis*, 20-80 (50-70 μm in length) cilia originate from each cell. The cilia touch one another almost throughout their length and look like a complex cilium. The orientation of cilia in the complex cilium, parallel or perpendicular to the plane of beating, ensures a thrust of maximum force, moving the veliger upward. The efficient beating of straight cilia is directed downward and coordinated by the wave of beating running throughout the ring clockwise. In the reversed upward movement, the cilia are geniculate.

The postoral ciliated ring of the velum also plays some role in veliger locomotion. This ring consists of a single row of complex cilia 15-20 μm long. Each complex cilium consists of four or five simple cilia. Their beating is effectively directed upward and counteracts the beating of the cilia of the preoral ring (Waller, 1981).

At moderate speed, the veliger expends nearly 10% of its entire energy for locomotion. Locomotion at higher speeds increases this expenditure up to 50% (Zeuthen, 1947).

The veliger moves upward with a fully extended velum and rapid ciliary beating. As intensity of beating decreases, the veliger sinks slowly. The sinking rate increases when the cilia of the velum stop beating. The rate is highest when the velum is rolling and shell valves are closed. Rolling of the velum is effected by two to four pairs of larval muscles, the

velum retractors. They extend from the shell posterior to the hinge line. In *Dreissena polymorpha*, the dorsal retractor passes along the dorsal side of the larva and supplies muscle fibers in the dorsal region of the velum which are attached to the velum integument. The medial retractor proceeds forward from the site of insertion to the ventral and medial regions of the velum. One fascicle is attached to the apical plate while the remaining fascicles are attached to various areas of the anterior part of the velum (Meisenheimer, 1901). In *Cerastoderma edule*, the medial and ventral regions of the velum separate retractors (Creek, 1960). During the rolling of the velum, first the apical plate withdraws into the shell and then the lateral parts of the velum apparently roll up and the shell valves close. Valve opening, muscle relaxation, and fluid filling the extensive cavity of the velum ensure its extension.

Veliger ascent usually follows a spiral pattern. This type of locomotion is seen in *Ostrea edulis, Mercenaria mercenaria, Dreissena polymorpha*, and others. In other species (*Argopecten irradians*), the veliger ascends in a vertical line, rotating like a flying cannon ball. The nature and speed of veliger locomotion depend on change in salinity, temperature, and pressure (Mileikovsky, 1973b; Cragg, Gruffydd, 1975; Hidu, Haskin, 1978; Cragg, 1980).

The veliger of *Mercenaria mercenaria* ascends at a speed of 7-80 cm min^{-1} (Turner, George, 1955; Carriker, 1961), the late veliger of *Crassostrea virginica* at a maximum speed of 60 cm min^{-1} (Wood, Hargis, 1971), and the veliger of *Lyrodus pedicellatus* at 45 cm min^{-1} (Isham, Tierney, 1953).

Bipinnariae swim by means of ciliated bands—the preoral, but more so the postoral. The water current created by these bands enables capture of food particles and concomitantly locomotion of the bipinnaria. In this case, the preoral lobe is directed forward. In the bipinnariae of sea stars family Asteriidae, the size of the processes increases with bipinnarial growth and they transform into long movable arms. Posterolateral and posterodorsal arms become the longest (Gemmill, 1914; Kume, Dan, 1968). Since the ciliated band extends over the elongated processes of the bipinnaria, the total length of the band increases considerably.

In many sea stars, however, the ciliated band on the arms is not well developed and does not participate in food capture; it functions only in larval locomotion. Beating of cilia on the arms is directed from the base to the tip of the arm. The rate of movement of bipinnariae of *Asterias rubens* is about 2 cm min^{-1} (Konstantinova, 1966). Reverse movement of the bipinnaria is not achieved by reversing direction of ciliary beating (as in the pluteus), but rather by the larva turning around. The bipinnaria executes a turn during swimming through contraction of dorsal muscles, which produces considerable flexion of the larva on the dorsal side (Strathmann, 1971). Movement of giant bipinnariae of *Luidia ciliaris* and

L. sarsi occurs through contraction of muscles in the elongated anterior part of the larva; ciliated bands of the larvae of these species (unlike *L. foliolata*) apparently do not participate in locomotion (Tattersall, Sheppard, 1934; Strathmann, 1971).

Nervous system and sense organs

In the veliger, the cerebral ganglion lies under the apical plate of the velum. Initially, the cerebral ganglion is a single composite structure but later becomes bilobate. Two large pedal ganglia in the midpart of the ventral side of the larva become joined through connectives with the cerebral ganglia. Development of pedal ganglia precedes pedal growth (Meisenheimer, 1901; Cranfield, 1973a).

The main sensory organ of the veliger is the apical plate, which may be drawn in, forming an apical pit. The pit diameter in *O. edulis* is 10-15 μm. Its anterior part contains 20-100 cilia, 6-8 μm long, which perform a sensory function (Waller, 1981). The apical plate in *Teredo navalis* bears only three complex cilia. Evidently, cilia of the inner preoral ring also perform a sensory function. These are small cilia, about 20 μm long, arranged regularly (Waller, 1981).

It was earlier assumed that larvae of sea stars possessed a diffuse nervous system under the epithelial cover (Gemmill, 1914; Tattersall, Sheppard, 1934). While investigating the nervous system of the bipinnaria of *Pisaster ochraceus* by glyoxalic method and electron microscopy, Burke (1983c) observed no such plexus but demonstrated the presence of axonal tracts at the base of the ciliated band and in the esophagus and two types of nerve cells situated in the ciliated band, one linked to the axonal tracts and the other provided with cilia. Clusters of nerve cells are present in the lower lip, in the corners of the larval mouth. Numerous serotonergic nerve cells have been detected along the ciliated band in the bipinnaria of *Asterias amurensis* (Nakajima, 1987). Right in the stage of dipleurula in the larvae of sea stars, catecholaminergic neurons arise in the nervous system from the commencement of its formation. The branches of these neurons enter the nerve stems under ciliated bands, the circumoral nerve ring, and plexus in the region of the ventral esophagus. It has been suggested that catecholaminergic neurons facilitate coordination of ciliary activity during capture, transport and absorption, or splitting of food particles in larvae (Nezlin et al., 1984; Dautov, Nezlin, 1990). The various behavioral processes in larvae of sea stars are independent of each other and the larval nervous system represents a complex of regulatory systems facilitating different reflexes (Dautov, Nezlin, 1990). Bipinnariae do not have developed sensory organs; however, it is quite possible that ciliary nerve cells of the ciliated bands perform a sensory function (Burke, 1983c).

Shell

The veliger is protected from unfavorable external influence by the cells of the outer epithelium. The shell represents the main protective formation. Like other larval organs, it simultaneously performs several functions: protective, supportive for muscle attachment, and jet-directing. However, protection is the primary, often basic function. The shell is a product of the activity of secretory cells of the shell gland. The peripheral cells of the shell gland secrete through its narrow opening the primary unpaired organic periostracum (Kniprath, 1979) which initiates veliger shell formation, i.e., prodissoconch I. X-ray diffraction analysis showed only amorphous matter of the periostracum present in the region of the future shell in the early gastrula stage of *Ostrea edulis*. Commencement of shell formation is indicated by subsequent manifestation of calcite and aragonite crystals (Medakovic et al., 1989, 1997). Soon after eversion of the shell gland, the shell bends along the mediodorsal line and becomes bivalved.

The shell grows rapidly due to marginal activity of the growing mantle and entirely covers the larval body in the early veliger stage. This concludes formation of prodissoconch I. Valves of the latter are usually uniform in size, calcified, and transparent. There is no calcification on the dorsal side at the place of their attachment, however, and this area of the shell constitutes a thickened periostracum. The hinge margin is straight and usually (except in mytilids) nondentate. The valve is D-shaped.

The cells of the free margin of the external mantle fold and the thickened margin of the mantle under the hinge continue to discharge a secretion from which a new section of the larval shell is formed—prodissoconch II. The latter differs from prodissoconch I in hinge development, appearance of lines on the shell surface, and a change in shell shape. The most significant change in shell shape is the appearance of umbones on both valves of the shell. Umbones are arranged dorsal to the hinge margin. Like prodissoconch I, prodissoconch II is also calcified; prodissoconch II of *Planktomya henseni* is an exception (Allen, Scheltema, 1972).

Data on shell sizes of larvae of 16 bivalves were studied in our laboratory for quantitative evaluation of the degree of adaptation of larvae to pelagic life. For this purpose, the ratio of larval shell length to adult was taken. The larval shell is a modified definitive organ whose development has shifted to the larval period. Thus, a high relative length of larval shell suggests greater maturity and greater emphasis on direct development. Thus, if the degree of development of ciliated rings (such data are extremely scarce) is positively corerelated to larval adaptation to pelagic life, the extent of shell development suggests an opposite tendency. This view is further supported by positive correlation between size of prodissoconch I and egg size, as demonstrated by Thorson (1936). This correlation is seen even at the intraspecific level (Goodsell, Eversole, 1992) and is confirmed by a similar correlation of egg size with length of hinge

of the larval shell, i.e., provinculum (Goodsell et al., 1992). Larval size and size of the egg from which it developed can be determined from the size of prodissoconch I; the size of the contracted larval velum in the shell can be judged from the size of prodissoconch II (Waller, 1981). Planktotrophic larvae of bivalve mollusks develop from eggs 40-85 μm diam and bear prodissoconch I 70-150 μm broad. The width of prodissoconch II holding the velum ranges from 200 to more than 600 μm. In lecithotrophic larvae, at egg diam 90-200 μm, the width of prodissoconch I ranges from 135 to more than 500 μm but the width of prodissoconch II is insignficant in view of poor velum development (Thorson, 1950, 1961; Ockelmann, 1965b; Berkman et al., 1991).

Larvae of *Crenomytilus grayanus*, *Crassostrea gigas*, and *Uizuhopecten yessoensis*, all with relatively small shell length, remain in plankton for 4-6 weeks while larvae of *Musculista senhousia*, *Hiatella arctica*, and *Kellia japonica* with relatively greater shell length reside in plankton, under very similar conditions, for 1-3 weeks. The larva of *K. japonica* is lecithotrophic while that of *M. senhousia* may be protected by the mother organism in the early developmental stages.

However, the ratio of larval shell length to definitive shell is not always an adequate measure of the pelagic adaptability of bivalve larvae. The high relative length of the shell of teleplanic larvae may be due to the need for locating a massive velum under its protection (Scheltema, Williams, 1983). Since the larval shell is visible even in shells of dead mollusks, a comparison of the structure, mineral composition, and microstructure of shells of living and dead mollusks is helpful in understanding the characteristics of their ecology and reproductive strategy (Lutz, Hidu, 1979; Lutz et al., 1980, 1984; Jablonski, Lutz, 1983; Fuller, Lutz, 1988, 1989; Lutz, Kennish, 1992).

Shell valves are closed first of all by the working of the anterior adductor. It is initially situated behind the dorsal edge of the velum and is the most prominent of the veliger muscles. The anterior adductor is formed and functions also in those larvae whose adults have only a posterior adductor developing later. Besides the adductor, velum retractors and three lateral muscles are attached to the valves; they extend from the valves in the region of attachment of the anterior adductor and veliger muscles and terminate in the body wall (Cragg, 1985).

Rudiments of definitive organs

In addition to functional organs, the veliger body contains rudiments of definitive organs that develop later and begin to function after the larva has settled to the bottom. Sometimes, rudiments of certain larval organs are also present but not developed in the veliger since they function only in the later larva, i.e., pediveliger. The first group comprises rudiments of

gills, renopericardic complex of organs, some elements of the nervous system, rudiments of the foot, byssus gland, some sensory organs and the reproductive system. In some mollusks, feet, byssus gland and sensory organs (eyes and statocysts) are seen only in the later period of larval life, reduced later, and hence are treated as larval organs.

Development of sea stars from planktotrophic larva may proceed in two ways. In most sea stars, there is a brachiolaria stage immediately following the bipinnaria, during which development of organs of attachment and anchoring of the definitive body of the organism are characteristic. Metamorphosis concludes with larval attachment to the substrate. In sea stars of families Luidiidae and Astropectinidae, organs of attachment do not appear during development; instead, the entire development of the definitive sea star and the conclusion of metamorphosis take place in the planktonic stage of bipinnaria. Such, in particular, is the development of *Luidia ciliaris* and *L. sarsi* (Tattersall, Sheppard, 1934; Wilson, 1978), *Astropecten aranciacus*, and *A. scoparius* (Horstadius, 1939; Oguro et al., 1976). In these sea stars the brachiolaria stage is lacking. Hence, rudiments of all organs of the definitive sea star are seen in the late bipinnaria of Luidiidae and Astropectinidae.

The organizing center for formation of the definitive organism is located in the region of the middle left coelom. We shall discuss metamorphosis in detail below. In other families of sea stars, rudiments of definitive organs that serve no functional purpose in the larva are only slightly developed in the bipinnaria. These are the five lobate processes of the coelom that appear in the late bipinnaria in the region corresponding to the left hydrocoel, i.e., rudiments of radial canals of the ambulacral system. In the developed bipinnaria of most sea stars, rudiments of temporary organs of the brachiolaria, such as brachiolar arms and attachment disk, appear in the preoral stage.

Pediveliger and Brachiolaria

The bivalve larva attains maximum size in the pediveliger stage and bears a functional foot with which it can creep while simultaneously retaining its ability to swim by means of its developed velum. Feeding, respiration, material transport, and excretion do not differ significantly in the course of development from veliger to pediveliger.

The brachiolaria differs from the bipinnaria in the presence of organs of attachment, large body and its processes, and pronounced formation of the definitive body of the sea star. Feeding, transport of substances, respiration, and excretion occur in the brachiolaria as in the bipinnaria. Barker (1978b) has described the ultrastructure of the integumental epithelium and coelomic lining of brachiolariae of *Stichaster australis* and *Coscinasterias calamaria*. In the region of the brachiolar style, cells of the

external epithelium contain numerous vacuoles and microvilli. The plexus of axons underlain by the basement membrane lies under the epithelium. Under the basement membrane is a layer of connective tissue. The inner basement membrane separates the coelem lining from the connective tissue. Longitudinal muscle fibers internally adjoin the inner basement membrane. The coelomic epithelium lies deepest and is comprised mainly of flat epithelial cells. These cells sometimes have pseudopodial processes and long isolated cilia.

Locomotion

The organ of swimming (velum) attains maximum development in the pediveliger stage. In addition, a new locomotory organ, the foot, begins to function. Like most larval organs, the foot too is a multifunctional organ. Its primary function is to probe the substrate for settling and attachment of the larva. The foot develops as an ectodermal outgrowth on the ventral side of the body between the mouth and anal opening. The heel of the foot (metapodium) begins to develop early and is covered with short cilia. Ventral to it in the pediveliger lies the toe (propodium), which later becomes considerably larger than the metapodium. Between the propodium and metapodium lies a depression into which the duct of the byssus gland opens. A furrow extending along the entire length of the foot divides it into two equal halves. According to Creek (1960), the larval retractor of the foot is functional in the pediveliger of *Cerastoderma edule*. The retractor is replaced by definitive structure once the larva has settled on the bottom.

The foot is covered with a ciliated epithelium. Each ciliary cell is covered with numerous microvilli. Cilia are irregularly arranged on the foot surface but are dense and very long at its tip and on the ventral and ventrolateral surfaces (Lane, Nott, 1970). Various subepidermal glands assisting in foot movement over the substrate and in formation and attachment of byssus filaments occupy the maximum volume in the pediveliger foot.

Swimming pediveligers generally exhibit a negative phototaxis and positive geotaxis and densely inhabit near-bottom water layers. During swimming the larva may thrust its foot out which, on contact with the substrate, initiates larval locomotion, namely, creeping. The sequence of locomotory acts during creeping are: 1) the slightly relaxed and extended foot moves over the substrate by means of cilia. Glands opening on the sole exude a secretion that contains weakly acidic mucopolysaccharides of low viscosity. Smeared on the substrate, this secretion facilitates ciliary movement. 2) The anterior part of the foot is temporarily attached to the substrate by means of a protein secretion released by another gland opening at the tip of the foot. This gland has been reported in pediveligers of *Ostrea edulis* and *Mytilus edulis* but is lacking in the pediveliger of

scallop *Placopecten magellanicus*. Hence the latter larva is not attached to the substrate during creeping (Gruffydd et al., 1975). Contraction of the posterior part of the foot hauls the larva forward. 3) The foot relaxes and the locomotory cycle is repeated after a few seconds. Creeping results in the attachement of the larva to the substrate or hauling of the foot followed by loss of contact with the substrate and resumption of swimming (Lane, Nott, 1970).

Locomotion of the brachiolaria is performed by cilia in the ciliated band. As the body processes grow, the size of the band increases and the processes usually become long flexible arms. The elongated ciliated band enables the brachiolaria to continue swimming as the definitive star develops. Movements of the brachiolaria become more rapid and complex. The larva may reverse directions not only by describing a loop through flexion of the dorsal side of the body, but also by changing the position of its arms. On encountering an obstacle, the brachiolaria extends its posterolateral, posterodorsal, and postoral arms forward while the mediodorsal process turns ventrally. The forward water current generated by this action of the ciliated band reverses the larval direction. Flexion of the processes and arms of the brachiolaria occurs through contraction of muscle fibers connecting the processes with the larval body (Strathmann, 1971).

Nervous system and sensory organs

Elements of the nervous system associated with foot functioning are mostly developed in the pediveliger stage. Pedal ganglia connected by commissures constitute the terminal point of anterior pedal nerves passing along the tip of the foot and transmitting sensory impulses from ciliated sensory organs. Besides cerebral and pedal ganglia, visceral ganglia are also developed around the posterior adductor (Hickman, Gruffydd, 1971; Cranfield, 1973a).

The apical plate and sensory cilia situated on the foot, primarily the long mobile cilia on its tip, represent ciliated sensory organs of the pediveliger. Sensory cilia are also seen in the furrow and byssus duct of the foot.

In many pediveligers, statocysts and eyes are seen in the mantle cavity. A highly developed nervous system and sensory organs are characteristic of planktotrophic larvae which dwell a long time in plankton. The planktotrophic pediveliger of *O. edulis* has two openings (7-9 μm diam), one on each side of the base of the foot, which lead into the statocyst cavity. These openings are encircled by two ciliated rings: short cilia 2-4 μm long and long cilia about 15 μm (Waller, 1981). A statolith forms in the statocyst cavity. The duct is later blocked and the statocyst becomes a closed vesicle. The statocyst duct is retained even in the adult *M. edulis*.

Here, not far from the base of the foot, two eyes are found in larvae of many species. Each eye is an almost round cup of pigmented epithelium filled with a gelatinous substance (Hickman, Gruffydd, 1971) and covered with a transparent crystalline lens. The eyespot in *Mytilus edulis* and *Modiolus modiolus* is 10 μm in size (Schweinitz, Lutz, 1976) and in *Tiostrea lutaria* 26-34 μm (Chanley, Dinamani, 1980). Nerves to the statocysts and eyes originate from the cerebral ganglion. Bayne (1971) described a band a ciliary cells passing from the roof of the mantle cavity to visceral ganglia in the pediveliger of *M. edulis*. This structure has been termed an osphardium, i.e., a chemosensory organ that assesses the quality of water entering the mantle cavity.

In addition to the above-described nervous system of the bipinnaria, a neuropyle-axon plexus develops in the brachiolaria, which is situated apically, at the base of the brachioles and under the epithelium of the adhesive papillae and disk (Barker, 1978b; Burke, 1983a). An accumulation of serotonergic neurons is also seen here (Bisgrove, Burke, 1987). Nerve cells of papillae and brachioles are connected with processes from the preoral nerve strand. Among the cells of papillae and disk, Barker identifies neurosecretory cells that presumably participate in attachment and adhesion of the brachiolaria to the substrate. Brachioles and papillae in brachiolariae of sea stars *Asterias rubens* and *Patiria pectinifera* are innervated by catecholaminergic neurons that perform a sensory function, judging from their morphology—apical process with cilium and branches from the basal part into the nerve stem (Nezlin et al., 1991).

Shell

In the pediveliger stage, prodissoconch II markedly enlarges, the hinge system develops, and the number of teeth increases. In addition to the anterior adductor, a posterior adductor develops behind the visceral ganglion above the hind gut (Cragg, 1985).

Attachment apparatus

The byssus gland develops rapidly and begins to function in the pediveliger. It forms as a depression in the ectoderm along the midline of the foot in the region of the pedal ganglia. The byssus gland or, more precisely, byssus complex, comprises a series of glands producing different secretions that facilitate formation and attachment of byssus threads to the substrate. The pediveliger may contain other glands in the foot in addition to those of the byssus complex. Gruffydd et al. (1975) divide the pedal glands of pediveliger into three groups: 1) glands producing very thin primary and secondary byssus threads, 2) glands producing mucus on the tip and sole of the foot which facilitates creeping, and 3) glands present in the larva but funtioning only after metamorphosis; they produce

a secretion for attachment of shell or secondary byssus threads to the substrate.

Cranfield (1973b, c) identified five phases in the behavior of pediveligers of *O. edulis* during settling. These, in his opinion, represent the sequence of hierarchic, fixed motor reactions leading to the final act of cementing. In the absence of stimuli specific for a particular phase, response is not produced and the larva returns to an earlier phase of settling. During settling, the pediveliger changes from ciliary to muscular mechanism of locomotion over the substrate; in this case, viscosity of the mucopolysaccharide secretion increases and secretion of byssus threads begins. At the end of settling, the secretion produced cements the larva to the substrate. The initial exploratory stages of pediveliger behavior during settling were described above. In the pediveliger of *O. edulis*, later, in the course of settling, muscular movements of the foot become sharper and stronger and the speed of locomotion decreases. Body turns occur more often in locomotion. Initially, the larva creeps in a straight line, rarely turning. Later, with increased frequency of turning, the angle of the path of movement decreases; the pediveliger track resembles a star and then a circle. In the last phase of settling (cementing), the oyster pediveliger rests on the foot and the larva rotates on the foot attached to the substrate by its tip and left valve. Coon and Boner (1985) reported similar processes during settling of the *Crassostrea gigas* pediveliger. The larva, ready to settle, after having swum with contracted foot, now extends it forward during swimming. It then drops to the bottom and moves over the substrate, executing a series of typical sliding movements. If the substrate is suitable, the larva cements itself to it permanently and metamorphoses into a juvenile oyster. In oyster *Ostrea edulis*, primary settling proceeds by means of cement secreted by the pedal gland and secondary settling by means of a similar material secreted by the inner mantle fold. In the later stages of metamorphosis, the settled organisms secrete a cement contained in the extrapallial fluid and the periostracum (Harper, 1991; Yamaguchi, 1994; Medakovic et al., 1997).

The attachment system of a brachiolaria typically comprises three brachiolar arms, an attachment disk and lateral papillae. Lateral brachiolar arms appear only in the brachiolaria stage; the medial arm is a modified medioventral process. During transformation into a brachiole, the medioventral process in sea stars of order Spinulosida (for example, *Acanthaster planci*—Henderson, Lucas, 1971, and *Patiria pectinifera*—Mortensen, 1921; Kasyanov, 1977) is subjected to less change than in sea stars of order Forcipulatida (for example, *Asterias rubens*—Gemmill, 1914, and *A. amurensis*—Kume, Dan, 1968). The axocoel processes enter the brachiolar arm. The preoral ciliated ring extends laterally on each brachiolar arm. These arms are crowned by a ring of attachment papillae which serve in probing the substrate and temporary attachment to it.

Neurosecretory and sensory cells are present in the papillary epithelium. Secretory cells predominate and produce a mucopolysaccharide-type secretion. Each such cell is armed with cilia and encircled by microvilli. Another type of secretory cell, devoid of cilia but covered with numerous microvilli, is sometimes observed. The characteristic feature of so-called vacuolated cells (these are probably secretory cells partially devoid of secretion) is the intracellular fibrils which extend from the basal part of the cell into the microvilli. The function of these structures is evidently supportive. Lateral papillae situated on each side of the attachment disk are identical in structure.

The attachment disk is a round, slightly concave structure comprising secretory cells covered with numerous branched microvilli. The protein secretion of these cells acts as cement for attaching the disk to the substrate. As in papillary cells, supporting fibrils are located in the disk cells.

While probing the substrate, the brachiolaria aligns itself by its ventral side, flexes its arms covered with the ciliated band, and attaches by one or two brachiolar arms contacting the substrate with their papillary crown. The brachiolaria, so to speak, walks along the substrate, attaching and detaching its brachiolar arms. Scouting may continue for a few seconds to one hour. If the substrate is not suitable for settling, the larva straightens its arms and swims away. If the substrate is satisfactory, the larva ceases scouting, alternately pressses its brachiolar arms to the substrate, spreads them maximally apart, then lowers the attachment disk to the substrate. A firm contact is ensured by the attachment papillae situated on each side of the disk. Cementation then commences, during which secretion of the attachment disk cells is released and binds the disk to the substrate. This process takes one to several hours. Metamorphosis, already commenced in the pelagic period of larval life, terminates in the attached state. After six to seven days, the juvenile sea star is dislodged from the stem of attachment by means of the primary ambulacral podia and, thus freed, begins an independent life (Barker, 1978b; Strathmann, 1978a).

Larvae of families Luidiidae and Astropectinidae possess no specialised larval attachment organs. For scouting the substrate and temporary attachment to it, the larva uses the already functional ambulacral podia of the juvenile sea star (Strathmann, 1978a).

Larval adaptations

In his article "Why Life Histories Evolved Differently at Sea", Strathmann (1990) stresses the differences in the evolution of life cycles of marine and land organisms. The evolutionary characteristics of marine organisms are associated with the specific processes of life cycles in the marine environment. Adaptation to its physical and chemical properties noticed in larvae of marine organisms differ considerably from adaptations to the

aerobic environment of spores, seeds, and other propagation stages—propagules—of land organisms although some essentially common features do exist.

Pechenik (1999) analyzed the favorable and adverse aspects of the presence of larvae in the life cycle of marine invertebrates. Since the direction of evolutionary changes in life cycles led, in general, to the loss of larvae, Pechenik pays special attention to the adverse consequences of the presence of larve. The futurity aspect of this problem is the potential effect of human activity on the direction of future evolutionary changes in the type of reproduction of marine invertebrates. According to Pechenik, the prevalence of larval development in contemporary marine invertebrates reflects more the difficulty of dispensing with the larva in the life cycle than preserving it (Pechenik, 1999).

Two basic features—settlement (Mileikovsky, 1977; Scheltema, 1981) and feeding (Strathmann, 1974a)—determine the basic tendencies of the evolution of planktotrophic larvae for which the water column serves as the "nutrient medium" as well as the carrier. Lecithotrophic larvae which do not require external nutrients lose adaptation to active feeding while partly maintaining a pelagic organization which enables them to remain in water for brief periods.

Adaptations of larvae to feeding and soaring which differ in taxonomically related groups, and even in related species, demonstrate the inadequacy of purely morphological approaches relating the evolutionary changes of ontogeny with phylogeny of the group and, for understanding them, call for a functional analysis of these modifications (Strathmann, 1988).

Two basic groups of adaptations of larvae to living in pelagic zones can be distinguished. The first group covers adaptations which involve locomotion in water and can be subdivided into passive and active (Kiselev, 1969). Passive adaptation results in reduction of specific weight and increase in specific surface. Reduction of specific weight among widely diverse pelagic organisms is the result of lipid accumulation, increase in water content in cells and intercellular space, and weight reduction of heavy skeletal structures. Specific surface increases as a result of reduction of body size and formation of various processes. Development of the locomotory apparatus represents an active adaptation.

Adaptation of planktotrophic larvae

Soaring in water is promoted by the small size of larvae and presence of large cavities filled with a gelatinous substance. Specific weight decreases due to accumulation of neutral lipids in the digestive gland of bivalve larvae and in the stomach of echinoderm larvae (Chia, Burke, 1978; Holland, 1978; Holland, Spencer, 1973). At the end of larval life, nutrient

reserves usually accumulate in mollusks and enchinoderms in the form of glycogen (Anderson, 1966; Holland, Hennant, 1974). Reduction of specific weight also promotes weight reduction of skeletal structures. Perforated spicules are often found in the echinopluteus larva while calcified shells are less visible in veligers than in spat; the shell of teleplanic veliger of *Planktomya henseni* is totally uncalcified (Allen, Scheltema, 1972). Various processes which develop in the larva of an echinoderm enlarge the specific surface of the body; possibly, these processes play the role of protecting it from predators (Pennington, Chia, 1984).[1] Their main purpose is to hold the ciliated rings and ensure efficient swimming and feeding of larvae. Ciliated bands or rings alternate during the development of cilia that cover the body of early larvae quite uniformly. Localization of long cilia (sometimes gathered into compact, dense cilia) along body margins in the form of a band surrounding larval processes facilitates more efficient ciliary functioning. Our comparison of data on the relative length of larval processes in sea stars and sea urchins of different phases of development confirms this conclusion.

Judging from larvae sizes of sea stars, pelagic organization is better developed in larvae of *Asterias amurensis* and *Distolasterias nipon* (and in larvae of other species of family Asteriidae) than in larvae of *Patiria pectinifera* (and in larvae of other species of family Asterinidae). This conclusion can also be drawn by comparing the ratio of length of larval processes to body length. In the bipinnariae of *P. pectinifera*, this ratio for the posterolateral process is 0.11-0.16, in the bipinnariae of *D. nipon* 0.15-0.19, and of *A. amurensis* 0.23-0.28. A comparison of these parmeters for brachiolariae is more striking; in the brachiolariae of *P. pectinifera*, the ratio of length of posterolateral process to body length is 0.08-0.14 and in *A. amurensis* 0.4-0.5. Thus, the aforesaid species can be arranged in the following sequence according to degree of development of pelagic organization of larvae: *P. pectinifera—D. nipon—A. amurensis*. This series is confirmed by the data of Dautov (1982) on development duration, which for *P. pectinifera* before settling is 25-30 days and for *A. amurensis* 60-70 days or more; in the case of *D. nipon*, it is known that the bipinnaria of this species is formed more rapidly than that of *A. amurensis*. On analogy with larvae of sea stars, the degree of pelagic organization of larvae of sea urchins can be evaluated. Species of sea urchins investigated in our laboratory by Kryuchkova (1987) line up according to length of pluteus I as follows: *Echinarachnius parma—Scaphechinus griseus—S. mirabilis—Strongylocentrotus nudus—S. intermedius—Echinocardium cordatum;* with respect to size of pluteus II: *S. griseus—E. parma—*

1. Like many other permanent zooplankton, larvae are almost not visible in water due to their transparency and even invisible sometimes (Greze, 1963; McFall-Nagi, 1996; Johnsen, Widder, 1998).

S. mirabilis—S. nudus—S. intermedius—E. cordatum; and for pluteus III: *E. parma—S. griseus—S. mirabilis—S. nudus—S. intermedius—E. cordatum.* In each of these series, sand dollars and heart urchins occupy the endmost positions with regular sea urchins intermediate. This gradation according to degree of development of pelagic organization of larvae agrees with data on time taken by them to attain pluteus I at +20 to +21°C (reliable information is not available on the duration of other stages for the species studied).

Thus, the degree of manifestation of pelagic organization of echinoderm larvae can be evaluated from size of the larval body and its processes, determined from the extension of the ciliated band along the perimeter of the body and its processes (Kasyanov, 1986a).

The greater the development of larval ciliated bands of echinoderms or rings in mollusks, the longer the course the larva can negotiate in the pelagic zone. Maximum development of the ciliated band occurs in transoceanic larvae (Scheltema, 1981; Domansky, 1984) and in larvae of deepwater species (for example, *Xylophaga atlantica*, Culliney, Turner, 1976). The presence of ciliated band or ring represents a major allomorphosis (according to Shmal'gauzen, 1983) in the evolution of pelagic larvae. Development of the nervous system and sensory organs in the larva is related to development of the ciliated band. Cilia of the band in the pluteus of sea urchin perform per se not only the locomotory role, but probably also, serve as rheoreceptors (Mogami et al., 1988). Interestingly evolution of the trapping apparatus of planktotrophic larvae proceeded in different directions in proto- and deuterostomatic organisms. The larvae of the former are characterized by ciliated bands with complex cilia branched from multiciliary cells and beat downward. Deuterostomatic larvae have simple cilia branched from monociliary cells and beat upward (Nielsen, 1994).

In different groups of the same type, a similar pattern of ciliature in planktotrophic larvae may evolve convergently; thus, judging from the composition of mitochondrial DNA, sea urchins are similar to sea cucumbers but not to brittle stars while the latter are more similar to stars (Smith et al., 1993; Strathmann, Eernisse, 1994). Thus, the similarity of the pluteus of sea urchins and brittle stars may be convergent.

As the larva grows and attains larger dimensions, new locomotory organs appear (ciliated epaulettes in echinopluteus larvae and vibratory lobes in echino- and ophiopluteus larvae) or ciliated rings as in transoceanic larvae of bivalves. Ciliary beating may ensure movement of relatively small organisms, usually up to 1 mm (Beklemishev, 1964). At these sizes, viscosity forces are more important than inertial. As the size of the larva increases, the role of inertial forces rises and larvae may effectively utilize active muscular movements (Cameron, 1986a): this

picture is observed in particular among some sea stars. The swimming of pediveligers of bivalves is facilitated by foot movement.

Ciliated bands or rings are multifunctional, like the original multifunctional constituents of their cilia. Cilia help in body locomotion, food capture, and sensory perceptions; they promote respiratory processes, transport of substances, and excretion. The performance of all these functions is also inherent to some extent in the ciliated organs of larvae.

The second group of adaptations is associated with the capture and transfer of food. Blastula and gastrula do not feed but survive on yolk reserves. The older larvae, however, take to active feeding. Ciliated band or rings are used as trapping apparatus.

The feeding larva has to generate a water current containing food particles, then grasp and move them to the mouth. Ciliary beating directed from the mouth of mollusk larvae and toward it in the larvae of echinoderms generates water currents. Cessation of beating induced by food particles holds them and, later, ciliated bands or fields transfer the food to the mouth. Among echinoderms, cilia of a single ciliated band (and two ciliated bands in bipinnaria of sea stars) filter the particles and facilitate larval swimming. Simultaneously, particles are transferred from the adoral band to the oral opening and, when so required, broken. In larvae of sea urchins facing food shortage, the length of the arm bearing ciliated bands extends, thus increasing the quantum of food gathered (McEdward, 1984). The ingestion rate of larvae of echinoderms increases with concomitant larval development as a result of elongation of its ciliated band (Fenaux et al., 1985b). Ciliated rings are more specialized in bivalve larvae; the preoral ring filters particles and serves as the main locomotory organ; the postoral ring filters and breaks particles; and cilia of the adoral ciliated ring transports them to the oral opening (Strathmann et al., 1972; Strathmann, Leise, 1979; Waller, 1981).

In some cases, the trapping function of the ciliated band displaces the locomotory function. In bipinnaria of *Luidia ciliaris*, the ciliated band on processes is transformed into furrows which catch and transport food particles. The larva advances by contracting the preoral lobe (Tattersall, Sheppard, 1934).

Adaptation of lecithotrophic larvae

The structure of lecithotrophic larvae is simplified by the absence of useless structures for larval feeding and adaptation of such larvae to pelagic zones is mainly associated with their dispersal.

Passive adaptation of lecithotrophic larvae to soaring in water is facilitated by their relatively small size and high lipid contents.

Powerful movements of lecithotrophic larvae are performed by ciliated band or rings, simpler than in planktotrophic larvae or, when such are

lacking, by cilia in ciliated fields. Evidently, the evolutionary development of the same pattern of ciliature in the form of 3-5 rings girdling larvae of sea lilies, larvae of some species of sea urchins and brittle stars, as well as larvae of Protobranchiata bivalves proceeded independently (Ivanova-Kazas, 1973, 1977a, 1978). In the doliolaria of sea lilies, soaring duration in plankton with 4 ciliated rings is only 1-2 hours thereafter the larva swims for 1-3 hours at the bottom in search of a suitable substrate and having found one by means of the minute apical tassel of the cilia, attaches and undergoes metamorphosis (Lahaye, Jangoux, 1988).

The ciliated cover of lecithotrophic larvae of brittle stars may be homogeneous as in *Ophionereis olivacea* (Byrne, 1991a) as well as in the form of transverse ciliated rings as in *O. annulata* and *O. squamulosa* (Hendler, 1982). According to Byrne (1991a), the uniform ciliated cover of *O. olivacea* is secondary in relation to ciliated rings of other brittle stars. Emlet (1994) points out that nonfeeding larvae less than 600 μm long usually have some transverse ciliated bands; such larvae, longer than 800 μm, are uniformly covered with cilia (the large ciliary area is probably necessary for active movement in water). The uniform ciliature of lecithotrophic larvae may be the result of heterochronism in the expression of ciliature pattern in the gastrula.

The lecithotrophic larva which has not shed its egg envelopes before metamorphosis loses adaptation to swimming. Thus, among bivalve larvae growing in egg capsules—*Lasaea rubra* (Oldfield, 1964), *Thyasira gouldi* (Blacknell, Ansell, 1974), and *Cardiomya pectinata* (Gustafson et al., 1986)—the velum loses its cilia and becomes a yolk sac.

Structural improvements for feeding and settling represent the main course of evolution of planktotrophic larvae. This improvement proceeds particularly through some specialized sections of ciliated cover and their further differentiation. Planktotrophic larvae of deepwater species, i.e., transoceanic larvae, develop maximum adaptability to pelagic survival. Lecithotrophic larvae are far less adapted to prolonged stay in pelagic areas. Direct development or lecithotrophic larvae can be seen in fairly advanced and specialized branches in the evolution of mollusks and echinoderms while they are characteristic of primitive groups, e.g., sea lilies, enchinothurid sea urchins and Protobranchiata bivalves (Ivanova-Kazas, 1973, 1977a, 1978; Raff, 1987). Does not the preceding statement show that most of the present-day lecithotrophic larvae have preserved the original type of larval development? Most zoologists and embryologists do not support this view (Jägersten, 1972; Ivanova-Kazas, 1977a; Strathmann, 1986). Supporting the conventional views on the evolution of life cycles of marine invertebrates (Ivanova-Kazas, 1995; Rieger, 1994), the assumption of original type, plesiomorphism, of the set of characteristics which may be regarded as lecithotrophic larval reproductive strategy is in my opinion erroneous (McHugh, Rouse, 1998; but see

Strathmann, 1993; Haszprunar et al., 1995). It remains to be added that in some gastropod mollusks and polychaetes which spend part or all of the larval period within the egg capsule, a transition is possible from lecithotrophic to planktotrophic while maintaining in lecithotrophically developing species the structure (and genes) of planktotrophic larvae. However, with the loss of these structures, the secondary development with actively feeding larvae in animals with lecithotrophic larvae or vivipary leads to the evolution of secondary larvae with a totally new set of larval organs that are not the same as the plesiomorphic set of organs of primary planktotrophic larva. There is no return to the past.

Lecithotrophy of primitive groups of larvae is perhaps a consequence of competition between old groups and those much younger on the evolutionary scale. The greater pressure of natural selection on old groups as new, more competent species appear may force the former to confine to less favorable ecological niches and, as a result, to a decrease in fecundity and failure of reproduction with planktotrophic larvae (Kasyanov, 1986a). Notwithstanding the differing views on the primacy of planktotrophy or lecithotrophy of larvae in different groups, it is generally acknowledged that a freely swimming larva (lecithotrophic or planktotrophic) is the primary form in the life cycle of marine invertebrates, the loss of larvae being a secondary phenomenon (Rieger, 1994; Havenhand, 1995; Byrne, Cerra, 1996; Hart et al., 1997; Nielsin, 1998; and others). Nielsen (1998) points out that had the larva been the primary form from which most multicellular organisms originated, metamorphosis should then be regarded as a much later acquirement of evolution. In my view, it is more probable that the formation and evolution of larvae and metamorphosis proceeded simultaneously from the primary pelagic-benthic life cycle.

Based on direct development, in exceptional cases, secondary larvae may have probably arisen; such is the case with lecithotrophic larva of sea star *Pteraster tesselatus* (McEdward, 1992, 1995). In fact, according to Harzprunar et al. (1995), the complex morphology of larvae and several examples of direct development, particularly in mollusks, suggest the possibility of the primacy of direct development. Based on concepts of adaptive significance of each new stage of development, Wolpert (1999) also assigns priority to the primacy of direct development. It must be pointed out that the palaeontological data on gastropod mollusks suggests lecithotrophic, not planktotrophic development as older in evolution (Chaffee, Lindberg, 1986). These investigators concluded that external fertilization is characteristic of primitive gastropod mollusks of the Early Cambrian; the diameter of their eggs was relatively greater and their development was lecithotrophic due to the small size of these mollusks. Strathmann (1986) found it difficult to reconstruct in this context the evolution of planktotrophic larvae among gastropod mollusks. The evolutionary sequence of alternation of developmental types in bivalves

is not clear (Jablonski, Lutz, 1983). Lecithotrophic larva of protobranchial bivalve mollusks, pericalimma, probably originated from lecithotrophic trochophores. Independent of the line trochophore-pericalimma, a veliger with trochophore as its predecessor evolved. The divergence of these larval groups arose as early as in the Ordovician (Gustafson, Lutz, 1992; Waller, 1998). At the same time, it may quite confidently be stated that planktotrophic development was primary in echinoderms (Strathmann, 1978a; Raff, 1987) with repeated changeover to lecithotrophic development in different phyletic branches. Concepts on the primacy of planktotrophic development in echinoderms with secondary replacement of it by lecithotrophic development in different lines finds support in recent works as well (McEdward, Janies, 1993, 1997; Wray, 1992, 1996; Wray, Bely, 1994; Hart et al., 1997). Loss of larvae especially in sea star, is accompanied by considerable simplification of embryogenesis (McEdward, 1992, 1995).

According to Ivanova-Kazas (1987a), planktotrophic as well as lecithotrophic larvae evolved from original atrochal, primarily lecithotrophic larvae similar to parenchymula and planula of present-day sponges and Cnidaria; actively feeding larvae appeared later with elongation of the pelagic phase and formation of larval organs for feeding and acquiring food.

On the whole, all variants of embryonic and larval development of bivalves and echinoderms ranging from modified lecithotrophy of primitive Protobranchiata mollusks or sea lilies to refined forms of larvae of *Planktomya henseni* or *Auricularia nudibranchiata* on the one hand, and direct development of sea urchin *Asthenosoma ijimai* or secondary larval development of freshwater Unionida on the other, present an amazing diversity and bear remnants of reproductive strategies of their lineage, they presently serve as a morphogenetic basis of reproductive strategies of present-day species.

Metamorphosis

At the conclusion of the pelagic life cycle, the larva should find a substrate, evaluate its suitability, and attach itself to it. Sensory cilia, eyes, and statocysts of bivalve larvae, sensory cilia and collection of photosensitive pigment in echinoderm larvae assist in finding and evaluating the substrate. Larvae or juvenile organisms attach temporarily or permanently by means of discharges from secretory glands present in the organs of attachment—brachioles of brachiolaria, primary tube feet of juvenile sea urchins, primary feet and tentacles of juvenile sea cucumbers, etc. (Cranfield, 1973a, b; Strathmann, 1978a; Kasyanov et al., 1983).

The degree of development of attachment structures and the selectivity of settling are ambiguously associated with manifestation of planktotrophy

in larvae. Among planktotrophic strategists, species with narrow selectivity for substrate are known, but more often larvae of such species settle on a wide range of susbtrates. Lecithotrophic strategists are characterized by high selectivity of substrate for settling.

Metamorphosis takes place over time after settling or before and is the result of structural deviations between pelagic larva and benthic imaginal organism. If the morphology of larva and that of the definitive organism has advanced far from the original type in the course of evolution, metamorphosis is regarded as catastrophic (Jägersten, 1972; Ivanova-Kazas, 1975; Chia, Burke, 1978). This type of metamorphosis is found in sea urchins (with the possible exception of cidaroid sea urchins, Emlet, 1987b), sea stars and brittle stars which are complicated by considerable disparities of structural patterns of larvae and definitive organisms. When divergence in structure of larvae and imaginal stage is not high and most larval organisms become definitive, metamorphosis is regarded as evolutive, for example in sea cucumbers or bivalves (Bayne, 1971; Jägersten, 1972; Chia, Burke, 1978). Further, in sea cucumbers, evolutive metamorphosis in all probability is secondary (Ivanov, 1985). However, the primacy of evolutive metamorphosis of sea cucumbers compared to the catastrophic metamorphosis of other echinoderms is based on Smiley's analysis of the metamorphosis of *Stichopus californicus* (Smiley, 1986). In any case, metamorphosis in species with planktotrophic strategy is manifest to a greater extent than in those with lecithotrophic strategy. Behavioral (settling) and morphogenic (metamorphosis) response of the larvae of marine invertebrates, like all other organisms, sets in after the preceding stages of development. Completion of these stages brings the larva into a competent state for settling and metamorphosis. This period of competence may vary significantly in duration in different species; for example, it is prolonged in bivalve mollusks of *Mercenaria* but short in those of *Mulinia* (Bachelet et al., 1992; Grassle et al., 1992) but settling and metamorphosis are impossible before its onset and after its completion.

Three features uniting the metamorphosis of larvae of all groups of bivalves and echinoderms independent of its nature need to be pointed out. Firstly, locomotory and food trapping organs in larvae are completely replaced by definitive organs, which in itself disturbs pelagic organization of larvae. Secondly, perhaps in all the groups under consideration, the course of metamorphosis in controlled by the larval nervous system (Chia et al., 1984; Bisgrove, Burke, 1987). In this context, mention may be made of electrical activity in larvae of sea urchins at metamorphosis (Satterlie, Cameron, 1985) and electrical stimuli at metamorphosis in sea urchins (Cameron, Hinegardner, 1974; Burke, 1983a) as well as induction of metamorphosis in gastropod mollusks by depolarization of the membrane of nerve cells in the presence of excess internal concentration of potassium ions (Yool et al., 1986) and mediators (Burke, 1983b; Morse, 1985). In

bivalve mollusks, metamorphosis and settling of competent larvae can also be induced by high concentrations of potassium in the medium (Nell, Holiday, 1986). Nitric oxide can possibly serve as an endogenous inhibitor of metamorphosis of mollusks. It inhibits pharmacologically induced metamorphosis in gastropod *Illyanassa obsoleta* while injection of nitroxide synthetase inhibitors helps competent larvae to become juveniles (Froggett, Leise, 1999).

A general feature of natural inductors of metamorphosis of the larvae of bivalve mollusks is perhaps the presence of a quinone or quinone-like ring in them (melanin LST-bacteria and quinone content in the protein of periostracum of oyster valves) or its possible formation by oxidation (catecholamines and phenol-containing proteins) (Estupinan, Waite, 1988; Chevolot, Cochard, 1989; Chevolot et al., 1991; Salas et al., 1989; Fitt et al., 1990). These inductors of metamorphosis act like external adrenergic agonists on sensory elements of the larval nervous system (Hirata, Hadfield, 1986; Coon, Bonar, 1987). As a result of the action of external inductors, endogenous catecholamines are liberated in larvae, triggering further processes of metamorphosis (Coon et al., 1988).

It may be pointed out that the chemical induction of metamorphosis shares many common features with chemoreception of adult marine invertebrates. Adult organisms are sensitive to concentration changes of low-molecular weight substances including peptides and amino acids that are important for seeking food, mate, and habitation site. Models of processes controlling transmission of metamorphogenic signals in larvae emerge from systems of olfactory responses of adults involving adenylate cyclase/cyclic adenosine monophosphate and phosphate kinase/inositol triphosphate pathways (Boettcher, Target, 1998).

Metamorphosis is ensured by the division of embryonic cells into cells of provisional larval organs and cells of definitive organs. Larval cells multiply rapidly, are differentiated and function intensively in the larval period. Intense functioning is achieved particularly by their polyploidy or fusion into multinuclear syncytia as, for example, in spiculoblasts of sea urchins (Okazaki, 1975; Isaeva, 1981; Kerkis, Isaeva, 1984). Imaginal cells remain undifferentiated and nonfunctional in the larval period. During metamorphosis, cells of larval organs perish or are redifferentiated into cells of definitive organs while imaginal cells emerge from the "dormant" state and, after a period of reproduction, are differentiated. The changeover of differentiation from the larval to imaginal program is regulated by neural and endocrine effects, but their mechanism has not been well studied. Succession of the nervous system of larvae and definitive organs is probably important for coordinating the processes of metamorphosis.

Strong morphogenetic movements in the course of metamorphosis are initiated by changes in the cytoskeletal cell system. In sea urchin *Lytechinus*

pictus, larval arms flex as a result of these movements and allow the definitive organism to come into contact with the surface; epithelial larval cells modify the body shape by compressing the tissues to the aboral surface of the young urchin; the former lining of the amniotic sac surrounds the tissues adjoining the aboral surface and forms the definitive epithelium (Cameron, Hinegardner, 1974, 1978). Compression of the larval epithelium is the result of modification of epithelial cells containing action microfilaments (Burke, 1985).

On transition from larval to direct development, the division of embryonic cells into the two groups ceases. In the development of brooding juvenile sea urchin *Abatus cordatus*, only one distinct period of cell multiplication is noticed at the end of embryogenesis and final formation of rudiments of definitive organs (Schatt, 1987).

Morphological reorganizations undergone by larvae of bivalves and sea stars in the course of metamorphosis shall now be studied in greater detail.

The *digestive system* of the pediveliger, with the exception of the trapping apparatus, undergoes insignificant modification (Bayne, 1971). The oral opening shifts to an anterodorsal position around the hinge line. The anal opening also shifts to a posteroventral position. The digestive gland acquires definitive structure.

In the brachiolaria, the ciliated band performs the function of the trapping apparatus as well as locomotory organ. In the course of metamorphosis, like the rest of the larval epithelium, it undergoes differentiation and resorption. Cells of the preoral ciliary band enter the stalk joining the forming star with the attachment disk; after metamorphosis, some species shed the stalk while others resorb it (Chia, Burke, 1978). The larval epithelium as a whole is not resorbed and the definitive outer integument of the juvenile star is differentiated from epithelial cells (after preceding dedifferentiation). The digestive system itself undergoes significant reorganization. Larval tissues of the mouth, partly gut and anal region are resorbed. Cells of the larval esophagus enter the outer epidermis and abdominal walls. A definitive esophagus is formed, the larval stomach reorganized and rudiments of pyloric appendages appear. The mouth opening appears on the oral side and anal opening on the aboral side of the juvenile star. The definitive gut with rectal glands forms from part of the larval gut (Gemmill, 1914).

Respiratory functions are taken over by the definitive from the larval epithelium.

In the course of metamorphosis of bivalves, the respiratory function is taken over by the branchial system from integumentary nonspecialized tissues. In most bivalves, the branchial system also functions simultaneously as an organ for food trapping. The number of gill filaments increases after metamorphosis (Bayne, 1976a). In many mollusks, mantle

margins fuse along the midline and muscular ducts—inhalant and exhalant siphons—are formed in front and back; they ensure and control water inflow through the mantle cavity.

Immediately after the mollusk settles, *transport of substances* within the organism proceeds in the same manner as in larvae. The circulatory system develops further. The larval *excretory system* disintegrates and is replaced by definitive nephridia originating from the pericardial cavity, which open through ducts into the mantle cavity.

Visceral coeloms formed from somatocoels, hemal and perihemal systems formed by means of the left somatocoel and axocoels participate in the transport of substances in the juvenile sea star. Spheroid bodies with phagocytes, axial organ and rectal glands participate in the elimination of metabolic products among echinoderms. Larval coeloms undergo considerable transformation. With their participation, a new locomotory organ, circulatory and perihemal systems, axial organ and coelomic cavity of the definitive sea star are formed.

The *locomotory apparatus* of veliger and pediveliger (velum) is invaded by phagocytes which absorb the velar cells. The muscular system which served the velum is also destroyed (Bayne, 1971). In *Placopecten megellanicus*, large parts of the velum are discarded during metamorphosis. Only the apical part is retained and participates in the formation of the upper perioral lobe (Culliney, 1975). As a result of these processes, larval mechanisms of swimming and food trapping disappear. Locomotory functions are usually passed to the foot and the function of food trapping to gills and perioral lobes; however, the foot of the mollusk also performs the role of trapping apparatus in juveniles (Reid et al., 1992).

Change in the food capture mechanism may require several days during which time the larva does not feed but uses its nutrient reserve. It is well known that a common feature of all larvae is the accumulation of nutrient reserves to ensure metamorphosis. These are concentrated in the hepatopancreas in the larvae of mollusks and in the form of elastic globules in the larvae of sea cucumbers (Chen et al., 1991) and others.

Successive phases of velum reduction and development of the gill system during metamorphosis have been studied in *Crassostrea virginica* (Baker, Mann, 1994). They demonstrated that interruption of feeding in the course of settling and metamorphosis extended not for a few days, as earlier presumed, but perhaps only a few hours and the larva continued to feed in the course of settling and metamorphosis.

The foot in burrowing mollusks develops further. Larval muscles of the foot are replaced by definitive organs. In the other, attached (sessile) species, the foot is totally or partly reduced and its cells are phagocytized (Hickman, Gruffydd, 1971).

With changeover to a benthic mode of life, the juvenile sea star loses its swimming organ, i.e., the ciliated band. The locomotory apparatus of

the brachiolaria, i.e., brachioles, is extremely transient and allows the sea star to move on a substrate. At this stage, the new mechanism of locomotion is tested by means of body processes terminating in papillary corona into which coelomic processes penetrate.

The definitive locomotory organ—ambulacral system, which arises during metamorphosis—works on a similar principle. The region of the left hydrocoel plays a leading role in its formation; bending, the two ends later merge and form the rudiment of the oral ring of the ambulacral system. Hydrocoelic processes branch out from the arc, i.e., rudiments of the radial canals of the ambulacral system. The terminal areas of these canals, together with the ectoderm surrounding them, later give rise to terminal tentacles while secondary processes forming along the canal sides represent rudiments of ambulacral podia. Axocoels participate in formation of the stone canal at the base of the larval pore canal (Gemmill, 1914).

The central *nervous system* of the pediveliger generally retains its structure. Visceral ganglia develop markedly and the relative size of cerebral ganglia decreases; pedal ganglia are reduced if the foot is reduced. In many, especially immobile species, eyes and statocysts disappear. The eyes of bivalve mollusk larvae undergo reduction in the course of metamorphosis and are transformed into thin bands of pigment, the latter preserved for a few days after metamorphosis (Baker, Mann, 1994). Ultimately, in all species the apical tuft of cilia disappears. In mobile forms, definitive sensory organs, lacking in larvae, are formed.

It is well known that the larval nervous system of the brachiolariae in sea stars in replaced by a definitive one in the course of metamorphosis. The first to degenerate are the catecholamine-containing disk cells, followed by neurons of lateral and mediodorsal processes and then papillae (Nezlin et al., 1991). Attention should be drawn to the suggestion of Nezlin et al. regarding neurotransmitters of the larval nervous system in sea stars, such as inductors of settling and metamorphism of the brachiolaria. This suggestion is based on the general principles of neurotransmitter control of development (Buznikov, 1987), indirect data for larvae of other groups of marine invertebrates (Coon, Bonar, 1985; Morse, 1985; Beiros, Widdows, 1995), and the fact of continuing synthesis of catecholamines in the course of metamorphosis of brachiolariae under conditions of breakdown of the larval nervous system (Nezlin et al., 1991).

The most developed ectoneural system in sea stars is formed from thickened ectoderm above the perioral ring and radial canals of the ambulacral system. Along with sensory organs disperced along the outer integument, numerous sensory elements are concentrated in the terminal tentacles and ocelli at the base of tentacles.

Changes in *shell* structure represent the concluding stage of metamorphosis in bivalves. The microstructure and mineralogy of shell change drastically and layers of new definitive shell—dissoconch—are formed. In many mytilid and some pectinid and other mollusks, after formation of the prodissoconch, the interdissoconch is formed in the course of settling and it is only later that the definitive shell (dissoconch) appears, which differs in mineralogy and microstructure (Fuller, Lutz, 1988). The shell of specialized forms such as those of wood-, and stone-boring mollusks and piddocks undergoes significant change (Kiseleva, 1970; Turner, Johnson, 1971; Boyle, Turner, 1976). The larval hinge is also replaced by a definitive one.

The definitive shell has a ligament that first appears in the prodissoconch and dissoconch (Lutz, Hidu, 1979). The ligament is an elastic cord connecting shell valves. It is formed in the ligament fossa of the shell. It should be pointed out that the ligament may not always be present in larvae; even if present, it does not always develop in the adult.

In species of family Teredinidae, new protective structures appear during metamorphosis: a calcified cone made of detritus over the inlet to the passage made by the mollusk; a calcified bed in the passage; and plates or palettes near the siphons (Turner, 1966). In two species of bivalves of family Pholadidae—*Zirphaea crispata* (Werner, 1939) and *Martesia striata* (Boyle, Turner, 1976)—a tooth and alveolus are formed on the ventral edge of the shell facing the umbo. This ventral hinge is used only in the period of metamorphosis and settling, after which it totally disappears.

Upon completion of metamorphosis, the attachment apparatus in mobile mollusks may become reduced (Broom, 1985).

The definitive skeleton has already begun to form in the bipinnaria of sea stars. As in all echinoderms, the skeleton of the bipinnaria of sea stars is internal and mesodermal in origin. The first skeletal plates—central, five radial terminal, and five interradial basal—form in the region of separation of the aboral disk of the definitive sea star. One basal plate becomes the madreporite, which closes the outer opening of the stone canal of the ambulacral system. Other elements of the skeleton appear later. In the juvenile sea star, all systems of the definitive body are found in various stages of development. These become fully developed as the sea star grows. Within a few days after metamorphosis, all these systems, except the reproductive, become functional.

On the whole, metamorphosis represents a distinct sequence of processes transforming the larva into a juvenile. A disturbance of this sequence or blockage of any stage leads to deformity or mortality of the organism (Turner, 1976).

REPRODUCTION

Formation and Differentiation of Sex

The reproductive system of bivalves and echinoderms develops in close association with coelomic derivatives which later take part in the formation of the excretory system: such proximity facilitates the release of gametes from the organism. The reproductive system is formed and competent in animals with planktotrophic and especially lecithotrophic strategies from the early stages of ontogenesis. In species with lecithotrophic strategy, early functioning of the reproductive system is evidently associated with their early maturity, which triggers reproduction of the organism.

Gonadal Development

Bivalves. Sex determinants in the egg cytoplasm were detected only in one family of bivalves—freshwater family Sphaeriidae (Woods, 1931, 1932). In the course of oogenesis, perinuclear accumulation of mitochondria shifts into the vegetative hemisphere of the oocyte. During egg cleavage this accumulation is noticed in blastomeres CD, followed by D, 4d, and finally in the two primary germ cells discernible in the stage of late blastula. Division of these cells leads to the formation of germinal anlagen in the form of two groups of cells on the ventral side of the pericardial rudiment. Hermaphroditism and vivipary are characteristic of Sphaeriidae. Such an early separation of primary germ cells has not been observed in any marine bivalve.

Gonadal development generally follows the development of other systems in the organism and occurs after completion of metamorphosis. Primary germ cells lie in the posterior region of the body ventral to the pericardium, near visceral ganglia and nephridia. Development of gonads and genital ducts proceeds in close relation with development of the excretory system (Tranter, 1958).

In *Mercenaria mercenaria,* the early gonad is covered by a single layer of coelomic epithelium. A lumen is formed in the gonad from the time of distinct manifestation of gonia. As in many species of marine bivalves, the juvenile gonad is bisexual with spermatocytes or sperm in the lumen and oogonia in the periphery (Loosanoff, 1937). In 1-2 mm specimens of *Venus striatula,* paired gonad rudiments merge along the median line and form a thin layer of cells between the body wall and posterior wall of the stomach. The lumen in the gonadal cavity is seen first in specimens of shell length 2.0-2.5 mm. In year-old mollusks at shell length 2–4 mm, the gonad already has acini in which male and female gametes at different stages of gametogenesis are present (Ansell, 1961). In *Crenomytilus grayanus* at shell length 15 mm, the gonad is represented by a system of tubules in which processes of spermatogenesis occur (Motavkin et al., 1971).

Gonadal development is similar in all Ostreidae—*Ostrea edulis* (Needler, 1932), *O. lurida* (Coe, 1943b), *Crassostrea virginica* (Coe, 1943b; Hayes, Menzel, 1981), *C. rhizophorae* (Nacimento et al., 1980) and *C. gigas*. After 1-8 weeks of larval settling, groups of primary germ cells present in the posterodorsal portion of the visceral sac ventral to the pericardium multiply and form strands of the primary gonad which are surrounded by mesodermal cells. These strands enter the connective tissue and grow under cover of the epithelium of the visceral mass. Gonadal strands together with connective tissue cells form gonadal tubes. Cells of tubes lying closest to the epithelium of the integument are differentiated into ciliary cells. Gonia are concentrated on the opposite wall of the tube. In *Crassostrea gigas*, 1-2 weeks after settling the gonads have such a structure. At this stage of gonadal formation, gonia are sexually differentiated. Gonadal tubes branch and form an anastomosing system lining the visceral mass. Outgrowths of the inner wall of gonadal tubes are formed perpendicular to the body surface. Developed outgrowths transform into acini of definitive gonads. In oysters aged 6-12 weeks, after settling, gonads are bisexual; in the gonad, gonia can be differentiated into oo- and spermatogonia but some gonia fail to differentiate; a few follicular cells are also present. Gonia are not differentiated at the growing ends of gonadal tubes (Dolgov, Kasyanov, 1984; Dolgov, 1987).

Echinoderms. To date, not a single case of early isolation of germ line has been detected in echinoderms. Sex determinants, nuage I type, in the form of accumulations of mitochondria and electron-dense bodies associated with them mark the primary germ cells and gonia in holothurians (Smiley, 1988) and sea urchins (Reunov et al., 2000). Later, while preserving nuage I type in previtellogenous oocytes, one more marker line of germ cells, nuage II type, arises; this line is represented by very fine electron-dense granules in a homogeneous matrix surrounded by a ring of mitochondria. From commencement of vitellogenesis, nuage are dispersed, which is not surprising for eggs of regulative development (Smiley, 1988). Sex determinants in the form of perinuclear bodies, present sometimes together with porous plates and mitochondria, were detected in oocytes (Afzelius, 1957; Harris, 1967; Aizenshtadt, 1986), spermatogonia (Houk, Hinegardner, 1981) and primary germ cells (Houk, Hinegardner, 1980) of sea urchins. These perinuclear bodies consist of accumulations of granular-fibrillar material.

Sea Cucumbers. Investigations devoted specifically to gonadal development in sea cucumbers have not been found in the literature. On analogy with known facts about the development of gonads in other echinoderms, the mesenchymal nature of gametes has been suggested. The early germ cells in sea urchins are found at the site of gonadal formation, in the mesentery of bivium (CD-interradius) between the stone canal and foregut (Clark,

1898). It is known that the genital ring is not formed in sea cucumbers from genital rachis and only tubules of a single gonad are formed by the migration of gonocytes. In very small (4-5 mm long and 0.3-0.5 mm thick) sea cucumbers *Rhabdomolgus ruber*, gonad anlage has been detected at the pentactula stage; in the stage of 5-6 tentacles, a lumen is seen in the gonad and the gonoduct begins to form (Menker, 1970). Smiley (1986) detected no gonad anlage either in the course of metamorphosis or immediately after it in *Stichopus californicus*, a typical representative of sea cucumbers with planktotrophic larvae. In this species, gonadal development commences 3-4 months after metamorphosis; mitosis of oogonia occurs in the inner epithelium of tubules of such gonads (Smiley, 1988). In sea cucumber *Synaptula hydriformis*, epithelial collar flagellate cells represent early germ cells; their apical-basal polarity becomes the primary polarity of the egg (Frick, Ruppert, 1996).

This author has studied the development of gonads in sea cucumber *Eupentacta fraudatrix*. In cucucmbers 4 mm long, gametes were already detected in the gonad primordium. The gonad lies roughly at the level of the madreporite embedded in the body cavity on the dorsal side in the dorsal mesentery between the body wall and stomach wall. At this stage, the gonad has the shape of an irregular ellipsoid or cluster of 5-10 small tubes formed as a result of development of individual lobes of the ellipsoid. Gametes are represented by gonia (gonial mitoses have been reported time and again) and early previtellogenous oocytes. Much later oocytes as well as spermatocytes have not been detected in gonads. In 7 mm long sea cucumbers, a group of gametes was detected in dorsal mesentery outside the gonad. This fact may suggest the ability of gametes to migrate into the dorsal mesentery in the period of gonadal formation.

In 12 mm long cucumbers, vitellogenous oocytes with a nucleus bearing marginal nucleoli are seen. Previtellogenous oocytes and gonia lie between large oocytes, along the wall or at the center of tubules. Gonial mitoses are seen. Vitellogenous oocytes are surrounded by follicular cells, evidently originating from accessory cells of the gonad. Another set of accessory cells accumulates granules, which are similar to granules of cells of gonad walls. It is possible that these cells feed and transfer nutrient reserves from gonad walls to the oocyte. The gonad acquires a definitive structure. It is significant that not one of the 20 juvenile cucumbers studied histologically had male gametes. It is possible that *E. fraudatrix* is characterized by a sex change very similar to *Cucumaria laevigata* (Hyman, 1955). The described patterns of gonadal formation in the course of normal development resemble the corresponding ones during regeneration (Kille, 1939).

On the whole, *E. fraudatrix* is characterized by early development of the gonad, which has already attained definitive structure by 1-2 months of age. Early gonadal development is also seen in other echinoderms

with lecithotrophic larva or direct development (Delavault, 1966; Chia, 1968a; Menker, 1970). Patterns similar to those described above can therefore be anticipated in sea cucumbers with lecithotrophic larva, large egg size, and low fecundity (Kasyanov, 1985b).

Sea stars. Delavault (1966) did not succeed in detecting sex determinant in large (about 500 μm diam) eggs or in blastomeres of sea star *Asterina gibbosa*. Primary germ cells were detected only on the eleventh day of growth, in late lecithotrophic brachiolariae, in the region of the duct connecting the hydrocoel to the environment. Primary germ cells, as in other sea stars, give rise to a genital rachis in *A. gibbosa*. It is distinguishable in juvenile sea stars with R = 1.5 mm (R is the distance from the center of the disk to the end of the ray). In *A. gibbosa* with R about 5-6 mm, gonads are present in each ray in the form of dense sacs held in the gonad sinus (MacBride, 1896).

While studying the development of young sea stars of *Leptasterias hexactis*, Chia (1968a) detected primary germ cells before commencement of metamorphosis. These cells lay above the dorsal horn of the left somatocoel, later penetrated into the axial sinus, and migrated from the aboral part of the axial organ right up to its middle. The ultimate fate of these cells was not traced; as the author could not find a relationship between primary germ cells and the gonad, he assumed that the gonad is evidently developed *in situ* from the epithelium of the hypogastric coelom.

In sea star *Asterias rubens*, with planktotrophic larva, the gonad primordium initially develops as a group of primary germ cells in the wall of the dorsal horn of the left somatocoel or adhering to it. This is the picture at the end of metamorphosis. Later, this group of cells forms a dense collection of cells growing in between the coelomic lining of the dorsal part of the body and axial sinus. Cells of the dorsal horn, surrounding the primary germ cells, with growth constitute the wall of the aboral or genital sinus. The accumulation of gametes extends into the genital rachis forming, in the course of growth, a genital ring along the inner surface on the aboral side of the test. The ring forms two branches in each interradius. These branchlets, encased in branches of the genital sinus and falling on each side of the interradial septum, represent gonadal primordia of the sea star (Gemmill, 1914). Gonadal formation in sea stars with lecithotrophic larvae, *Asterina gibbosa*, *Solaster endeca*, and *Crossaster papposus* (Mac-Bride, 1896; Gemmill, 1920), proceeds in a generally similar manner.

Genus *Patiria* is very close to genus *Asterina*. In the Atlantic *A. gibbosa*, however, the eggs are not many, yolk-rich, and development proceeds with lecithotrophic larva; in *Patiria pectinifera*, on the other hand, eggs are numerous and the larva planktotrophic. A comparison of data on gonadal development in these species, differing in fecundity, egg size, and developmental characteristics, would be worth-while.

In *Patiria*, with R = 4-5 mm, gonads are lacking in rays. At the site of future gonads, the coelomic lining at the base of interradial septa appears thickened, evidently as a result of the ingrowth of the coelomic sac of the future gonad, originating from the dorsal horn of the left somatocoel. Gametes can be seen in the region of the stone canal in the form of a free rudiment surrounded by coelomic epithelium, proximate but not touching the axial organ.

Primary germ cells penetrate the gonad of *Patiria* at R = 7 mm. Gametes enter the gonad from the aboral genital ring forming branches in interradii toward gonad sites. In sea stars of such size, gametes may be seen in the gonad, in the aboral genital ring, and in its branches; in the case of smaller sea stars, they are seen in the region of the stone canal. Gonads and genital primordium in the region of the stone canal consist of gonia and the so-called accessory cells. Gonads do not appear simultaneously in all rays. Viewed from the aboral pole, gametes fill gonads clockwise from the interradius of the stone canal. In the aboral genital ring, free gonia, sometimes in a state of mitosis, are visible.

In *Patiria* with R = 12 mm, two layers of coelomic epithelium can be distinguished in the gonad. These layers, representing the gonad wall, separate the genital coelom or sinus from the coelom *per se*. The gonad, consisting of 1-2 layers of gonia with large vesicular nuclei, is encased in the sinus. The degree of gonadal development in different rays and even within the same ray differs.

Comparing our data on gonadal development for *P. pectinifera* with literary data on gonadal development for *A. gibbosa* and other sea stars, it can be concluded that in stars with planktotrophic larva, penetration of primary germ cells into gonad primordium and attainment of a definitive structure by the gonad proceed later than in sea stars with lecithotrophic larva (Kasyanov, Kolotukhina, 1985a).

Sea urchins. Gonadal development in sea urchins proceeds as in sea stars. MacBride (1914) detected primary germ cells in sea urchin *Echinus esculentus* in the period of metamorphosis and assumed that they arose from the wall of the left posterior coelom. Houk and Hinegardner (1980) describe a group of primary germ cells in the dorsal mesentery in the region of the stone canal, first detected in the period of metamorphosis in sea urchin *Lytechinus pictus*. This group of cells later forms the aboral ring from which genital primordium of the gonad proper originates in interradii as an outgrowth. Until this moment the gonad primordium comprises only branches of genital hemal sinus originating from the dorsal horn of the left somatocoel. In juvenile urchins 1 mm diam, primary germ cells and precursors of accessory gonad cells migrate from the genital rachis to the gonadal formation site. Unlike in sea stars and brittle stars, the annular aboral genital rachis in sea urchins exists only in juveniles and disappears in adults. Branches of hemal genital sinus transform into main hemal

gonad vessels. The capillary network formed by these vessels is later visible on the gonad surface (Okada, 1979).

In juvenile sea urchin *Strongylocentrotus intermedius* with test diam 5-6 mm (age 200 days) produced under laboratory conditions, sex-undifferentiated gonads are in the form of thickenings of coelomic epithelium. In the cavities of the latter, Naidenko and Dzyuba (1982) isolated three types of cells which included round cells about 5 μm diam with vesicular nucleus and containing dispersed chromatin bodies and 1-2 nucleoli. Like Houk and Hinegardner (1980), Naidenko and Dzyuba considered these cells primary germ cells and observed their mitotic division in gonads.

Processes of development and differentiation of gonads were also studied in juvenile sea urchin *Strongylocentrotus nudus* (Varaksin, 1980). In urchins of test diam 6 mm, gonads were in the form of simple unbranched sacs. Gonocytes 7.5-8 mm in diam represent cells with vesicular nucleus fringed with cytoplasm.

Sex Differentiation and Sex Ratio

Genes responsible for sex differentiation in mollusks and echinoderms have not been identified. It has been demonstrated, however, that some regulatory genes responsible for sex differentiation (especially controlling sex-dependent differentiation of neuroblasts in development and transcription of yolk protein genes) are common for fruit flies and nematode *Caenorabditis elegans* (Raymond et al., 1998). The presence of similar genes can be anticipated in genomes of mollusks and echinoderms as well.

Bivalves. Coe's (1943a) classification of sex states in mollusks divides bivalve species into ambisexual (hermaphroditic) and gonochoristic (different sexes). Among hermaphroditic species, Coe distinguishes species with functional hermaphroditism, with multiple rhythmic sex change, with single sex change, and with unpredictable sex change. Coe's classification, while demonstrating the diversity of sex states among mollusks suffers, in our opinion, from excessive specificity for describing different species. In actuality, depending on conditions, many species may be either gonochoristic or hermaphroditic while a single change of sex may in some species be replaced by variable sex change.

Interestingly, with sex change, sexual behavior likewise changes but lags behind compared to morphological restructuring (Galtsoff, 1964).

Gonochorism might perhaps be found only among mollusks with planktotrophic larva. To confirm gonochorism in a given species, information is required about the sex state of the young. However, hermaphroditism may be noticed as a random event even among gonochoristic species.

During functional hermaphroditism, processes of oo- and spermatogenesis may proceed simultaneously in the gonad. Normal functional hermaphroditism is characteristic of some species of genera *Pecten, Kellia, Thracia, Teredo, Lasaea,* and others (Beauchamp, 1986; and others). In *Tridacna squamosa,* sex formation is probably the outcome of a combination of successive and simultaneous hermaphroditism (Dolgov, 1987). Most such species are characterized by fertilization in the mantle cavity and development bypassing planktotrophic larva, under protection of the mother organism. Functional hermaphroditism may be random yet found sometimes in many species of bivalves with planktotrophic larva, more often in the first year after maturity or in mollusks of the oldest ages. Motova (1979) recorded random simultaneous hermaphroditism in *Swiftopecten swifti* (male and female gametes found in the same acini of gonads) and in *Crenomytilus grayanus* (male and female gametes present in different acini). Hermaphroditism of this type had been noted earlier by Sadykhova (1973) and Kutishchev and Drozdov (1974). According to the latter investigators, the proportion of hermaphrodites in *Crenomytilus grayanus* could takedown 2.5%.

Multiple rhythmic sex changes are widely known since this phenomenon is characteristic of European oyster *Ostrea edulis* (Roughly, 1929; Orton, Amirthalingam, 1931; Coe, 1943a) as well as shipworm *Teredo navalis* (Coe, 1943b). In these species, the female phase changes into the male phase, again into the female phase, and so on. The sex change may occur many times in the course of a single season of reproduction. In ontogenesis, such a cycle usually commences with the male phase, i.e., protandry is characteristic of these species. Species exhibiting repeated rhythmic sex change usually care for the brood, i.e., their development proceeds partly or wholly in the mother organism.

A one-time sex change is widely prevalent among bivalves, including species with planktotrophic larva; animals exhibit hermaphroditism at the time of sex change. This phenomenon, found in several bivalves, is particularly characteristic of *Mercenaria mercenaria, Swiftopecten swifti, Mizuhopecten yessoensis,* and *Bankia setacea* (Loosanoff, 1937; Coe, 1943a; Mori et al., 1977; Motova, 1979). The predominance of sequential or simultaneous hermaphroditism in bivalve mollusks may depend on population structure. Thus, in old settlements of *Tridacna squamosa* of varying age, sequential hermaphroditism is common while in pioneer settlements with populations of the same age and size with low density, simultaneous hermaphroditism is the norm. In very similar populations of high density (for example, under conditions of marine culture), the species behaves like a gonochoristic one (Dolgov, 1991). A one-time sex change in stationary colonies of *Crenomytilus grayanus* and *Mytilus edulis* comprising many generations reveals protandry: gonochorism is noticed in the pioneer populations of these species (Dolgov, 1985; Dolgov et al.,

1987). A sex change of variable nature is also observed in genus *Crassostrea* with planktotrophic larva. Species of this genus may undergo sex variation or may even retain the same sex depending on habitat conditions: under adverse conditions, the proportion of males usually rises while under favorable conditions, the proportion of females increases (Amemiya, 1929; Needler, 1932; Butler, 1949; Bahr, Hillman, 1967; Davis, Hillman, 1971; Kennedy, 1983). The sex of oysters of genera *Ostrea* and *Crassostrea* is influenced by members of the same species that have settled alongside (Burkenroad, 1931; Buroker, 1983; Kennedy, 1983). Interesting data were reported for *Ostrea pulchana*. Young oysters, 2-26 mm shell height, settling on the edge of valves of much larger oysters invariably turned out to be males in the reproductive season. These young oysters subsequently detached and became females; among oysters with shell height over 25 mm, males comprise only 3% (Calvo, Morriconi, 1978).

Dolgov (1984) studied the dependence of sex differentiation in juveniles of *C. gigas* on the presence of members of the preceding generation. Differences were detected in the nature of sex differentiation and sex ratio among juveniles of *C. gigas* settled on shells of living oysters of the preceding generation and those settled on empty valves of scallops which had not colonized priorly. In the first case, among juveniles 10-11 months old, males predominated; females were detected only in a collection with a high density of spat per specimen of the preceding generation. In populations of the second type, the ratio of sexes in juveniles was close to one. Definitive males and females were noticed among juveniles aged 1-1.5 months after settling; hermaphrodites constituted about 1%. Oogonia and oocytes were found in gonad sections of hermaphrodites along acinar walls; cells of the spermatogenous series were seen in the gonad lumen. Differentiation of female sex usually proceeded without the protandrous phase. Thus, sex differentiation of juveniles of *C. gigas* is regulated by members of the older generation but the mechanisms of this influence are not known.

The possibility of sex change in ontogenesis among larva-producing oysters of genus *Ostrea* with repeated sex change and in oysters of egg-producing genus *Crassostrea* with variable sex change is ensured by the presence of gonocytes of both sexes in the gonad (Galtsoff, 1964). Evidently, for marine bivalves as a whole, there is a view that what should be considered is not the initial differentiation of undetermined gonocytes (Lucas, 1975), but the predominant multiplication and subsequent differentiation of oo- and spermatogonia in response to environmental conditions. In juvenile gonads, cells of a sex different from that of the gonad are found not only in species with sex change in ontogenesis, but also in gonochoristic species (Loosanoff, 1937; Coe, Turner, 1938; Ansell, 1961).

Early functioning of the reproductive system is termed juvenile sexuality

(Lucas, 1975). Because of considerable differences in the fecundity of juvenile and large mature specimens, participation of the former in reproduction cannot significantly influence the population level but contributes to maintaining its gentic diversity. This function cannot be served later by most juveniles because of their high mortality.

Sea cucumbers. Very little information is available on sex differentiation and its variations in sea cucumbers. According to Ackermann (1902), tubules developing at the base of gonads in *Cucumaria laevigata* are not differentiated initially but in the course of gonadal development produce female gametes. Later, after some duration of functioning, oocytes are resorbed and spermatogenesis commences in the same tubules. As a result, the gonad consists of short undifferentiated tubules, very long female, and even longer male tubules. Hermaphroditism is also encountered in some cucumbers, among them *Cucumaria crocea*—ova as well as sperm cells are formed in the same tubules (Lüdwig, 1898). Among Aspidochirotida, hermaphroditism has been recorded in *Mesothuria intestinalis* (Hyman, 1955).

Hermaphroditism is not rare in Synaptidae (Clark, 1907) in which planktotrophic larvae are absent. We detected hermaphrodite gonads in two species of this family from the South China Sea—*Euapta godeffroi* and *Synaptula* species (Kasyanov et al., 1989). In both species, late oocytes enveloped in a jelly coat were found in the same gonad tubules with mature sperm cells organized into spermatocysts.

In general, as in other groups, hermaphroditism correlates with lecithotrophy and brooding. Of nine brooding cucumber species, at least four were hermaphrodites; of four viviparous species of Synaptidae, three were hermaphrodites (Ghiselin, 1969).

Brittle stars. Brood care in brittle stars usually involves bearing embryos in pouches. Most species of brooding brittle stars are small in size and simultaneous or protandrous hermaphrodites (Hendler, 1979, 1991). During protandry, transition from male to female sex usually does not involve the stage of hermaphroditism (Byrne, 1991a, b).

Sea stars. Cognetti and Delavault (1962) classify sea stars into three categories: stable gonochoristic, labile gonochoristic and hermaphroditic species. Hermaphroditism is characteristic among others, of *Asterias forbesi* and for some species of genus *Asterina*—*A. batheri*, *A. gibbosa*, *A. minor*, *A. panceri*, and *A. phylactica* (Hyman, 1955; Delavault, 1966; Kano, Komatsu, 1978; Komatsu et al., 1979; Strathmann et al., 1984). In some regions, *A. gibbosa* and *A. batheri* may be hermaphroditic and in others gonochoristic. *Fromia ghardaquana* (Delavault, 1966) and *F. milleporina* (Kasyanov et al., 1989) also have hermaphroditic gonads. Gonadal tubules of *F. milleporina* are filled with spermatozoa and growing oocytes lie along the walls of tubules, suggesting protandry in this species. Protandry has

also been noticed in *Asterina gibbosa* and *Asterias rubens* (Mortensen, 1938; Brusle, 1970; Vinberg, 1970) and protogyny in *Asterina panceri* (Ohshima, 1929). Of the three sympatric species of genus *Patiriella* with embryonized larval development, two species, *P. gunni* and *P. calcar*, with lecithotrophic brachiolariae were found to be gonochoristic while *P. exigua* laying eggs on the substrate followed by development of highly modified demersal brachiolariae, is protandrous or, in some cases, a simultaneous hermaphrodite. It should be pointed out that male dwarfism is characteristic of the last of these species (Byrne, Barker, 1991; Byrne, 1992). Potential hermaphroditism is also found in gonochoristic species, e.g., *Asterias rubens*, *Leptasterias groenlandica*, *Marthasterias glacialis*, and *Echinaster sepositus* (Delavault, 1966). Such species are treated as labile gonochoristic. Electron microscopy showed the presence of early oocytes along with spermatocytes in the gonads of males of these species (Delavault, 1975). Most species of sea stars investigated are stable or labile gonochoristic. On the whole, hermaphroditism and labile gonochorism are often come across in species with lecithotrophic larvae and stable gonochorism in species with planktotrophic larvae.

In *Patiria pectinifera* studied by us—a species with planktotrophic larva—in the size group R = 15-19 mm, sex was differentiated in one male and one female with R = 18 mm. In 10 other sea stars, sex could not be differentiated from the preparations. In the size group R = 20-29 mm, the proportion of females averaged 26.2% for the year as a whole and males 28.4% while 45.3% of the sea stars could not be differentiated. Thus, the sex ratio from the commencement of sex differentiation of gonads in *Patiria* species was close to one. It must be pointed out that the maximum number of undifferentiated individuals pertained to the postspawning autumn-winter period when there are no differentiated gametes in the gonad. Sex-undifferentiated sea-stars are generally smaller in size than those identified as male or female.

In the size group R = 30-52 mm, the sex ratio is likewise close to one (on average for the year as a whole, 44.9% females for 49.3% males). The number of undifferentiated individuals is slightly less than in the preceding groups and averages 5.8%.

Thus, *Patiria pectinifera* is a gonochoristic species which, compared with the hermaphroditism of genus *Asterina*, confirms the assumption of a positive relationship between the gonochorism of a species and the presence of planktotrophic larva in it (Kasyanov, Kolotukhina, 1985b).

Sea urchins. The chromosomal mechanism of sex determination of type XY was noticed in sea urchin *Paracentrotus lividus*. This species differs from other species of sea urchins also in a small number of chromosomes (2n = 36)—sea urchins usually have 42-44 chromosomal pairs, and in nucleolar organizers in three pairs of chromosomes (Lipani et al., 1996). Houk and Hinegardner (1980) reported differentiated gonads in *Lytechinus*

pictus with test diam 3.3-60 mm; in females, gonocytes were enlarged in size and lost contact with the adjoining cells; the oocytes reached 25 μm diam and spermatozoa were noticed in males. Holland and Giese (1965) differentiated sex in juvenile sea urchin *Strongylocentrotus purpuratus* 16 mm diam. Ovaries contained oogonia and early oocytes while testes held spermatogonia. Experiments with thymidine tracer showed that DNA synthesis occurs in many oogonia, preleptotene oocytes and spermatogonia. In *S. intermedius* raised in the laboratory, sex was discernible even in specimens 7-8 mm diam (age 238 days); their gonads contained stray oo- or spermatocytes (Naidenko, Dzyuba, 1982). Spermatozoa were detected in gonads of urchins 10 mm diam and ova in urchins 20 mm diam (age 300 days). According to Vasaksin (1980), *S. nudus* is characterized by protogyny since the gonads of urchins 6 mm diam contained isolated oocytes. Their numbers increased considerably in urchins 28-30 mm diam but later oocyte mortality set in. In urchins of test diam 35-36 mm, sex was distinctly diagnosed. Maturity and complete development of gonads were recorded in urchins of test diam exceeding 40 mm.

Sea urchins are gonochoristic and hermaphroditism is seen only as a rare anomaly in *Strongylocentrotus droebachiensis, S. intermedius, S. pulcherrimus, Paracentrotus lividus, Echinus esculentus, Arbacia punctulata, Echinocardium cordatum, Echinarachnius parma,* and some other species (Moore, 1935; Boolotian, Moore, 1956; Herold, 1969; Achituv, Delavault, 1972). Hermaphroditism is manifest in that in the same specimen, some gonads function as ovaries and others as testes, or mixed gonads, ovotestes, are present (Harvey, 1939; Hyman, 1955). On the whole, however, hermaphroditism and sex change phenomena are not characteristic of sea urchins, due perhaps to the relatively less frequent lecithotrophic larvae, brooding, and other related features of reproductive strategy in them.

Gonochorism of marine bivalves and echinoderms with planktotrophic larvae

Data on the presence or absence of hermaphroditism were obtained in the course of studying annual gonadal cycles of 11 species of bivalves and 11 species of echinoderms (1 species of sea cucumber, 5 species of sea urchins, and 5 species of sea stars). Of the 2,858 histologically investigated mature animals (large specimens were generally chosen), only 7 were hermaphrodites: 1 hermaphroditic specimen each of *Swiftopecten swifti, Mactra chinensis* and *Aphelasterias japonica* and 4 of *Crenomytilis grayanus*.

Gonochorism is thus characteristic of the species investigated by us while hermaphroditism averages only 0.2%. Of the seven hermaphrodites detected, five are species with a sessile life style. Acini of hermaphroditic gonads may contain gametes of one or both sexes. In acini with gametes of both sexes, oogonia and oocytes are disposed along the periphery while spermatozoa predominantly fill the lumen.

Concluding the study of the problem of sex variation in bivalves and echinoderms as a whole, it may be pointed out that the sex of the young may not be the same as that of the same animal after attaining definitive maturity. Usually, juveniles function as males. A single sex change from protandry depending on the presence of members of an older generation (Hoagland, 1978; Dolgov, 1985, 1987) is a clear example of reproductive tactics of such species.

Multiple sex variation or functional hermaphroditism with perhaps self-fertilization may be seen in species with lecithotrophic strategy (Strathmann et al., 1984). Such variants of sexuality may be associated with energy limitations of these species: all specimens produce eggs and participate in maintaining the population level and there is no wasteful expenditure of energy on obligate males.

The proportions between the various variants of sex determination can be expressed as follows:

	Planktotrophic strategy	Lecithotrophic strategy
Gonochorism	++ -	+ -
Protandry	+ -	+ -
Protogyny	-	+ -
Functional hermaphroditism	-	+ -

Protogyny found among lecithotrophic strategists, for example in some sea cucumbers, does not make such a signficant contribution of the young to the gene pool of the population as protandry and hence is not found in species with planktotrophic strategy. Participation of small-size females in maintaining the population while being significant for species with lecithotrophic strategy, is not important for species with planktotrophic strategy having large females with great fecundity (fecundity increases in cubic proportion as the animal size increases).

The sex ratio may undergo sharp changes during asexual reproduction. Male to female ratio is 24 : 1 in brittle star *Ophiactis savignyi* inhabiting the brood canals of sponge *Haliclona* sp. Further, the insignificant sizes of brittle star eggs suggest planktotrophic development although the main course in this species is asexual reproduction (Chao, Tsai, 1995).

Well over a century ago Charles Darwin, referring to the problem of sex ratios, felt that "the entire question was complex and that its solution was a task for the future" (Darwin, 1874; from Darwin, 1953, p. 355). The future has arrived, more data have been gathered, and several hypotheses propounded, but the problem is nowhere near to being solved.

Maturity

Many bivalves and echinoderms become fully mature 1-3 years after

settling and attain such dimensions by that time that their fecundity is comparable to that of more adult specimens (Fuji, 1960b; Thompson, 1979). The age at maturity is a fairly labile parameter of the reproductive strategy. The possibility of a signficant reduction of age at maturity under favorable conditions (Naidenko, Dzyuba, 1982) and the phenomena of juvenile sexuality suggest the tactical importance of this parameter of reproductive strategy.

It would perhaps be more correct in the case of bivalves and echinoderms to refer not to the age, but dimensions at maturity, when the organism begins to expend a significant proportion of energy in the production of gametes. Adequate dimensions of reproducing specimens ensure high-calory food and low pressure from predators (Seed, Brown, 1978). Lawrence (1987) has given a table showing the dimensions of echinoderms at maturity.

Sexual dimorphism

This is an important aspect of reproductive strategy. By emphasizing the difference between sexes in somatic tissues, sexual dimorphism is developed in species with complex types of insemination and brood care. Among bivalves and echinoderms, sexual dimorphism is fairly sharply manifest in species which do not have planktotrophic larvae but exhibit brood care. Brood care, usually by females, calls for the development of organs specialized for this purpose or modifications of already existing organs. Different variants of vivipary and brooding in the groups under discussion have been described by Hyman (1955), Matveeva (1979), Sastry (1979), and Lawrence (1987).

Sexual dimorphism is the result of reproduction and differentiation of cells in target organs or tissues under the action of hormones and is manifest sometimes only in the period of reproduction. Manifestation of sexual dimorphism is weak in species with planktotrophic strategy and energy consumption in maintaining and generating it is clearly negligible compared to comsumption solely for gamete production.

It must be pointed out that differences between sexes are not confined to morphological manifestations but concern the physiology and behavior of the animal. Specialized sexual behavior prevails to some extent or the other in all species and the absence of morphological differences between sexes does not imply absence of differences in behavior even in animals which are generally less active, such as sessile bivalves. Thus, spawning in female *Crassostrea virginica* represents a more complex behavioral act (with the participation of gills) compared to spawning in males of this species (Galtsoff, 1964). Males of sea star *Archaster typicus* exhibit complex sexual behavior: they are capable of identifying females among members of the species by contacting them with rays and form pairs with identified

females at the time of insemination (Run et al., 1987). Examples of fairly complex sexual behavior are not infrequent among echinoderms.

Before spawning, echinoderms form groups which adversely affect production of germ cells due to limited food availability but promote success of insemination to a very large extent. Insemination of the eggs of sea urchins proceeds successfully in algal growths at a high density of males and females lying within 25 cm of each other (Wahle, Peckham, 1999). The proportion of inseminated eggs falls dramatically even at less than 1 m between one another (Levitan, 1991; Levitan et al., 1992; Wahle, Peckham, 1999). The picture is different among sea stars. In *Acanthaster planci*, insemination in nature proceeds even at 100 m between males and females. For insemination of the eggs of this star, a very small quantity of spermatozoa is perhaps adequate (Babcock et al., 1994; Banzie, Dixon, 1994).

Bivalves. Sexual dimorphism is manifest in a few marine bivalves and associated with brood care in species brooding limited offspring. Thus, the ventral side of the shell of female *Milneria kelseyi* and *Thecalia concamerata* has a septum for forming a chamber in which the young are borne, evidently after incubation in the ctenidium (Young, 1969).

Another distinct example of sexual dimorphism is male dwarfism. In family Galeommatidae, dwarf males have been detected in *Ephippodonta oedipus* and *Chlamydoconcha orcutti*. Male dwarfism arose through secondary brooding of juveniles under cover of the mantle of adult mollusks (Morton, 1976, 1981). According to Morton, dwarf males represent a temporary phase in the growth of these mollusks; they later develop into animals of definitive dimensions. In family Montacutidae, dwarf males have been found among commensal forms: *M. phascolionis* (Deroux, 1960), *Montacuta floridiana*, and *M. percompressa* (Jenner, McCrary, 1968). In the latter species, dwarf males are actually reduced to testes surrounded by the tissue of the female mantle. Dwarf males were recently detected in two species of teredinids, *Zachsia zenkewitchi* and *Z. serenei*, inhabiting the rootstock of grass-wrack (Turner, Yakovlev, 1981, 1983; Yakovlev, 1988). Yakovlev and Malakhov (1985, 1987) demonstrated that the organization of dwarf males of *Z. zenkewitchi* involves a combination of the features of neoteny, regression, and specialization.

A tendency of size reduction of males has been recorded in superfamily Astartoidea: shells of males in *Astarte elliptica*, *A. sulcata*, and *A. borealis* are smaller than in females (Sastry, 1979). In these species, planktotrophic larvae are absent. The phenomenon of male dwarfism has evolved in species living in a "coarse-grained medium" with little chance of finding partners of the opposite sex.

Sea cucumbers. From the brief description of sexual dimorphism in echinoderms, it can be seen that, as in marine bivalves, very few instances

of distinctly manifest sexual dimorphism are found; these are due not so much to the type of insemination or the phenomenon of mutual attraction of sexes, as to brood care.

Sexual dimorphism is not characteristic of sea cucumbers. It has been observed only in some brooding species inhabiting Antarctic waters. In these species, females can be distinguished from males in the presence of a brood chamber on the "dorsal" (*Thyonepsolus nutriens*) or crawling (*Psolus punctatus* and *Cucumaria paria*) surfaces. Brooding in genuine brood pouches is more perfect. Thus, in Antarctic sea cucumber *Psolus koeleri*, the anterior end is surrounded by five widely open pouches in the body wall. The next stage is development of internal brood pouches with narrow openings in the region of the crown of tentacles (Hyman, 1955). Thus, sexual dimorphism is well evidenced only in brooding species without planktotrophic larvae.

Sea stars. Sexual dimorphism is weakly manifest in sea stars with planktotrophic larvae although differences have been observed sometimes between sexes in color of body integuments. In family Astropectinidae, males of genus *Leptychaster* have many gonads in each ray with independent gonopore openings, while females have the usual pair of gonads with two gonopores. Sexual dimorphism is distinctly manifest in some brooding species. In family Brisingidae, females of *Odinella nutrix* lay eggs in basket-like formations at the base of rays of their spines. In females of many species of order Spinulosida, the dorsal membrane of the so-called nidamental chamber is well developed. Brooding takes place in this chamber (Hyman, 1955).

Male and female size is identical in most species but in *Archaster typicus*, *Astrochlamys bruneus*, *Ophiodaphne materna*, and possibly some other brooding species, males are smaller than females (Lawrence, 1987). Sexual dimorphism is very distinct in genus *Xyloplax* inhabiting at depth in flooded timber (Rowe, 1987).

Sea urchins. As in the preceding groups, sexual dimorphism in sea urchins is associated with brood care. Brood chambers are present in the peristomium or periproct of brooding females of cidaroid urchins in Antarctic waters—*Austrocidaris canaliculata*, *Ctenocidaris nutrix*, and *Stereocidaris nutrix* (Hyman, 1955; Baranova, 1968). In female sand dollar *Fibularia nutriens* (Cypeasteroida), brood chambers are located in petaloid ambulacral areas; the males of this species are smaller than females (Mortensen, 1948). In female heart urchins of genus *Abatus*, brood chambers are formed in four ambulacral rows (Kilias, 1969; Magniez, 1983).

In sea urchins with planktotrophic larvae, Hamann (1887) detected sexual dimorphism with respect to size and external shape of genital papillae. These papillae occur on the aboral side of the body on genital

plates (including madreporite) and represent distal sections of gonoducts covered with connective tissue and epidermis; they open into the tip of the gonopore through which gametes emerge during spawning; at the moment of gamete release, the gonopore widens considerably (Chia, 1977). Unlike most sea urchins, genital papillae in sand dollars Clypeasteroida are located not on genital plates, but on the margins of the large central madreporite or at some distance from it. This central plate arose in the evolution of clypeasteroid urchins as a result of the fusion of genital plates and Chia was not accurate in his statement that gonoducts in Clypeasteroida pass between the madreporite and genital plates (Chia, 1977).

Sex determination from papillae is possible only after the sea urchin has attained maturity (Okada, 1979). Okada in his study of *Hemicentrorus pulcherrimus* and *Echinometra mathaei* demonstrated that the sexual dimorphism of papillae is determined by factors arising from the proximal section of the gonoduct. This section of the gonoduct determines not only differentiation of secondary sexual characteristics, but is also responsible for the ability of the distal section of the gonoduct to perforate the genital plate.

While describing genital papillae in several sea urchins, Chia (1977) contradicted the presence of papillae in the females of many species analyzed by Tahara and his colleagues (1960). This group of investigators showed that the lack of papillae in the females of regular sea urchins is only seeming and attributable to the submergence of short papillae in depression on the body surface. Osanai (1980) described sexual dimorphism of four species of sea urchins inhabiting Hokkaido coasts.

The sex of regular sea urchins *Strongylocentrotus nudus* and *S. intermedius* can also be determined from the length of genital papillae (Kasyanov, 1984c). Our data in general agree with the observations of Osanai (1980) on these species and supplement them. It is probably for want of quantitative data that Osanai drew no conclusion regarding the high manifestation of sexual dimorphism of papillae in *S. intermedius* compared to *S. nudus*.

The sex of sand dollars *Scaphechinus mirabilis* and *Echinarachnius parma* evidently cannot be determined from external characteristics outside the period of gamete release. At the time of gamete release, papillae are greatly extended and become distinctly discernible in the background of short test spines (Kasyanov 1984c). An apparently similar picture is seen in *Dendraster excentricus* (Lawrence, 1987). The shape of papillae perceived at the time of gamete release is similar to that in sand dollar *Arachnoides placenta* (Chia, 1977). According to Chia, the long length of papillae in *A. placenta* protects the gametes from the abrasive action of sand grains; the same could be said of *Scaphechinus mirabilis* and *Echinarachnius parma*. Dense envelopes covering mature eggs of these sea urchins evidently

play an "anti-sand" role (Kasyanov et al., 1980). Chia (1977) may be correct in explaining the long length of genital papillae of male sea urchins as an adaptation for greater protection of spermatozoa, compared to large ova, from water currents generated by the integumental cilia.

Sex differences in sea urchins according to height of the test, color of body integuments or ambulacral tube foot on the oral side of the body, and some minor features of the disposition of gonopores on papillae or the disposition of papillae on the genital plate, have been reported in the literature. These differences are seen only in a few species, however. Sex differences between females and males can be determined from the size of genital pores on test plates (Tahara et al., 1960; Endelman, 1974; David et al., 1987) but this valuable feature is inapplicable for determining the sex of live specimens. It may be pointed out that under certain conditions the pattern of development in the sea urchin can be determined from the diameter of the gonopore and characteristics of the crystalline structure of genital plates (Emlet, 1987a).

In general, among bivalve mollusks and echinoderms with planktotrophic larvae, sexual dimorphism from external features is either not revealed at all or is perceived only on thorough observation. Further, structures manifesting dimorphism may be extremely variable in external shape and size.

Reproductive System

The structure of the reproductive system ensures reproduction, development, and maturation of gametes, their collection and release. For the growth and reproduction of gametes, the system has in it structures for inflow and storage of nutrients and their transferal to gametes.

The gonad wall in echinoderms plays the role of supportive structure and a typical "technical" floor. It is this wall that ensures the inflow of nutrients and oxygen, excretion of metabolic products, and resorption; nerve endings and receptors also lie here (Beijnink et al., 1984; Smiley, Cloney, 1985). Connective tissue elements of the gonad impart to it the required elasticity while muscular members facilitate evacuation of gametes during spawning. In bivalves, a part of these functions is performed by organs and tissues into which the gonad penetrates. For synchronizing the processes of gametogenesis, there are mechanisms which regulate these processes within the reproductive system as well as in response to stimuli arising from the organism and from the external medium. At the same time, in the reproductive system, signals (nerve or humoral) transmit back to the organism information on the course of metabolic and other processes in the gonad; this function is essential for synchronizing the various processes of the activity of the organism with the events occurring in the reproductive system and, particularly, for initiating at the appropriate time sexual or spawning behavior and

facilitating mating of gametes of opposite sexes. The cyclicity of gamete production in most animals requires development of temporary "work sites" for reproduction and growth of gametes and temporary "storage sites" for preserving them. Special structures present in the reproductive system ensure the release of gametes beyond the range of the system during spawning, with preliminary packing in egg envelopes or sperm balls. The latter have been described in bivalves with internal-external insemination: *Ostrea edulis, O. lurida, Corbicula* cf. *fluminalis* and *Codakia orbicularis* (Coe, 1943a; Alatalo et al., 1984).

The relatively simple structure of the reproductive system of bivalves and echinoderms is explained by the absence as a rule of internal insemination in these animals and hence special structures for performing this function.

Bivalves. The reproductive system of bivalves initially consists of two gonads and two gonoducts. Gonad tubes branch, anastomose, and perforate the connective tissue of the visceral mass of the animal. The terminal enlarged sections of these tubules are called acini. In the period preceding spawning, the gonad in some bivalves grows into the foot as in *Mercenaria stimpsoni* and *Spisula sachlinensis* and (or) into the mantle as in *Mytilus edulis* and *Crenomytilus grayanus.* During spawning, gametes released from the gonad pass through gonoducts which open into the nephridia as in sea scallops (from where gametes enter the mantle cavity) or directly into the mantle cavity as in Ostreidae (Quayle, 1969), Mactridae (Medvedeva, 1976), and Veneridae (Stickney, 1963). With rare exceptions (Le Pennec et al., 1984), the structure of male and female gonoducts is identical.

Gonad wall. The gonad lacks an epithelial wall per se; cells in gonad tubules are surrounded by connective tissue fibers accompanying the gonad during the growth period. A basal membrane underlies the connective tissue fibers. Since the gonad wall is underdeveloped in bivalves, the functions of providing nutrients to gametes and removal of metabolic products as well as release of gametes are performed by the tissue surrounding the gonad.

Echinoderms. In a typical case, the reproductive system consists of some (usually in multiples of five) or one (in sea cucumbers) gonads, gonoducts, annular genital rachis, the latter persisting in the adult state in sea lilies, sea stars, and brittle stars, as well as hemal and perihemal genital sinuses (Hyman, 1955). Through these sinuses, nutrients reach gonads, products of resorption of gametes pass and humoral contacts are established between individual gonads (Ch. W. Walker, 1982). Gonads of echinoderms enlarge significantly in the period of reproduction, sometimes covering much of the body cavity of the animal. Unlike bivalves, in echinoderms, gonads do not penetrate into other organs and are freely held in the body

cavity through attachment to its wall and other organs by layers of peritoneal epithelium.

Gonadal structure in sea cucumbers is primitive. The anterior part of the coelom has a single gonad comprising different members of branched and unbranched tubules with a single genital duct. The space-time relationship of organization of gametogenesis with changes in gonadal anatomy during the course of the annual reproductive cycle is well expressed in this class. Tubules along the base of the ovary represent a continuum of extremely small primary tubules in front up to the largest secondary ones at the rear. A cluster of primary germ cells lies in front of the primary tubules in the connective tissue of the gonad base. All primary tubules contain only oogonia; secondary tubules contain previtellogenic oocytes while vitellogenesis proceeds in the rearmost tubules. After shedding the germ cells, the last of the tubules degenerate and are later substituted by younger ones in front. Thus, a wave of gametogenesis proceeds in the gonad, its different stages occurring in the different chambers of the gonad (the tubules) (Smiley, 1988).

Sea stars have two gonads on each ray. Gonads are in the form of clusters or bundles of tubules. In primitive sea stars of families Luidiidae, Astropectinidae, and others, two rows of small gonads with independent openings or a single common one are present along each ray. In sea urchins, racemose or saccate gonads consisting of several bundles of short tubules are disposed in interradii. Regular sea urchins have five gonads which are reduced to 2-4 in irregular urchins. This reduction is the result of a disturbance of the radial body symmetry. In sand dollars *Scaphechinus mirabilis* and *Echinarachnius parma,* interradial arrangement of gonads is disturbed while only the positon of gonoducts is preserved. Four gonads together with the alimentary canal occupying the entire body cavity anastomose to form a single entity.

Gonoduct. In sea cucumbers, the gonoduct opens onto the dorsal side near the crown of tentacles or between them in a special genital papilla in the interradius (Hyman, 1955). We detected such a papilla notably in sea cucumber *Eupentacta fraudatrix.* In sea stars, gonoducts usually open onto the aboral side of the animal with a few pores between skeletal plates. In sea stars exhibiting brood care, gonoducts open onto the oral side of the body. In sea urchins, short gonoducts open onto the aboral side with gonopores in papillae passing through genital plates.

Gonad wall. In sea cucumbers, the gonad wall structure is comparatively simple. Peritoneal epithelium (epithelium lining the body cavity) covers the gonadal tubules. Tracts of axons of neurosecretory cells, which probably participate in the regulation of reproduction, are disposed in the peritoneal layer (Smiley, Cloney, 1985). Sinuses of the hemal system without epithelial lining pass under ciliary cells of the coelomic epithelium and myoepithelial

cells underlain by basal membrane. Connective tissue fibers are washed on one side by hemal fluid containing amoebocytes and, on the other, are in contact with gametes and accessory cells of the gonad itself.

The gonad wall in sea stars, sea urchins, and brittle stars is very complex. The literature provides no clear description of the origin of various cell layers and cavities forming the gonad wall and to understand its structure is problematical. The origin of its elements is therefore described below. In sea stars, sea urchins, and brittle stars, the primordium of the reproductive system, initially formed between dorsal and ventral horns of the somatocoel elongates into a genital rachis and later into a ring surrounded by a double coelomic pouch (or tubule) formed by the dorsal horn of the somatocoel. In other words, the genital rachis and, later, the genital ring is encased in a double tube. The space between the outer and inner walls of the duct represents the coelomic cavity and the space between the genital rachis and inner wall of the duct represents in origin the primary body cavity. During the course of development of the reproductive system, the genital aboral ring with the elements just described forms radial branches which represents the gonad primordium. These branches, originating from the ring pass under the coelomic (peritoneal) body lining and become the outer lining of the gonad. In origin, the space between the coelomic peritoneal lining and outer wall of the coelomic duct surrounding the outgrowth of the genital ring, also represents the primary body cavity.

Thus, taking into consideration the gonad wall from the center to the periphery, the gonad itself (more precisely, its gametes and somatic cells) is surrounded by the hemal sinus. The cavity of the hemal sinus is filled with fluid containing amoeboid cells and granulocytes; it does not have its own endothelium and is lined with a network of fine collagen fibers. This network performs the function of a basal membrane for the layer of gametes (Ch. W. Walker, 1982). Then comes the inner coelomic lining of the so-called perihemal space (i.e., the coelomic cavity accompanying the gonad). The outer coelomic lining of the perihemal space comes into contact with the connective tissue fibers and cells which fill the remainder of the primary body cavity. Myoepithelial cells lining the perihemal sinus bear flagella and evidently cause movement of the fluid contained in the perihemal space (Ch. W. Walker, 1982). Spicules present in the gonad wall of echinoderms are specific for different species (Rawlinson, 1932; Conand, 1981). Finally, there is a peritoneal layer consisting of four types of cells—epithelial flagellate, vacuolized, muscular, and nerve—in the basal membrane binding the outer side of the elastic connective tissue.

The degree of development of the component structures of the gonad wall varies from class to class (wall members in sea stars are the most distinct and best described) and in the gonadal cycle (the wall structure is more clearly descernible in gonadal preparations after spawning and at

commencement of intense gametogenetic processes). During gonad enlargement, the wall expands, the perihemal sinus usually becomes poorly distinguishable, and the inner lining of the hemal sinus and the layer of gametes on it often form outgrowths in the gonad cavity. Such outgrowths are particularly typical for testes.

Spatial Organization of Gametogenesis

Gametes lining the gonad inside and filling its lumen form neither a compact layer of cells nor constitute chaotic accumulation. They are arranged systematically in acini of the gonads and occupy definite positions in them in different stages of gametogenesis. Tubules or acini of gonads posses an internal structure which organizes the entire gametogenic process, supply and distribution of nutrients, hormone synthesis, release of gametes and hormones, and later prepares the gonads for a new cycle of gametogenesis. In the acinus, somatic cells of the gonad form specific connections with gametes. Spermatogenic columns of testes and ovarian follicles represent the structural unit of the acinus within which the gametogenic cycle proceeeds. As gametogenesis proceeds, the morphology of these structural entities changes, altering the complete cycle of development and extinction. Researchers term this the gonadal reproductive cycle. In the words of Walker (1974), somatic cells of the gonad "orchestrate" the events of the gonadal cycle.

Spermatogenic columns are formed by gigantic axial accessory cells extending from the wall of the gonad into its lumen. Spermatogonia, spermatocytes, spermatids and spermatozoa are disposed along the sides of the axial cell commencing from the base. Upon completion of spermatogenesis, the size of the columns decreases and free space is provided for the finished product, i.e., the spermatozoa. In the ovarian follicle, spatial relationships between gametes and accessory cells run counter to those observed in the testes. Follicular cells and their processes surround groups of oogonia and later individual oocytes. Thereafter, the entire process of oogenesis proceeds in the follicular cover: in the course of oogenesis, ovarian follicles are displaced from the gonad wall to its lumen. The same accessory cells may perform diverse functions and ensure the process of gametogenesis in the gonad (this has been better demonstrated in the testes). Accessory cells which represent structural organizers of the gametogenic process, also perform the function of feeding by transferring nutrients to gametocytes and control function by producing various hormones; they also cleanse the gonads of gametes by resorbing them (Walker, Larochelle, 1984). Accessory cells of the gonad in sea urchins which attain large proportions constitute an exception to this general rule. However, the spatial relationships of these cells with gametes and their performance of the characteristic functions of accessory cells confirm the general principle.

The general nature of gamete production as a flexible operation, very distinctly manifest in species with planktotrophic strategy, holds true even for species with lecithotrophic strategy. Development of a special phagocytic tissue is an interesting new development in sea stars with lecithotrophic larvae. This tissue resorbs the numerous gametocytes which have not completed gametogenesis. Nutrients are later transferred to those cells which have successfully completed gametogenesis. In this manner, phagocytic tissue participates in controlling the fecundity and transfer of nutrients.

Bivalves. The work of Drozdov and Reunov (1986a) on the ultrastructure of spermatogenesis in *Modiolus difficilis* is of interest. Accessory cells of testes (these may be called axial cells) have an extended form with numerous processes. They adhere by their base to the basal membrane of the acinus and their tip reaches the center of the acinus. The axial cell is laterally surrounded, commencing from the base, successively by spermatogonia, spermatocytes, and spermatids. Dense specialized contacts exist between some spermatocytes and the axial cell as well as spermatids and the axial cell. Such contacts also form between processes of adjacent axial cells in the acinus body. Thus, axial cells represent "organizers" of spermatogenic columns. Functions of axial cells are quite numerous and generally correspond to the functions of analogous cells described for testes of vertebrate animals under different names: Sertoli cells, feeding cells, cells of follicular epithelium, sustentocytes, and supportive cells. In *Scorbicularia plana*, axial cells of testes branch from the basal membrane of the acinus and connect with spermatogonia and spermatocytes to form a desmose-type junctions and with spermatids by surrounding them with their digitate processes. These axial cells are capable of phagocytosis and disappear toward the end of the spermatogenic cycle (Sousa et al., 1989).

The transfer of nutrients to testes for spermatogenesis has not been studied in bivalves. Nutrients evidently enter the acini of the gonad from the blood vessels adjoining it as well as from adipogranular and vesicular cells surrounding the connective tissue (Bayne et al., 1982).

The growing oocytes in the ovaries of some bivalves are held in the so-called follicular cover consisting of a thin layer of follicular cells flattened on the oocyte surface (Bernard et al., 1988). These follicular cells form the required structure of the acinus within which the nutrients are distributed for oogenesis and hormonal control of the latter is carried out.

In our view, the structure of gonads in species of bivalves in which the follicular epithelium has not been detected needs to be reinvestigated by electron microscopy. It is possible that the follicular cover is formed in these species not of bodies, but processes of somatic cells of the gonad.

In the different periods of the gonadal cycle, a large number of morphologically variable granulocytes and globulocyctes can be found in acini and additionally in the connective tissue. Accessory cells with

lipoprotein granules occupy a significant proportion of acini in *Mya arenaria* (Coe, Turner, 1938) and *M. japonica* (Dzyuba, Maslennikova, 1987a).

Accessory cells in acini of many animals resemble cells surrounding the connective tissue and possibly the two are identical. Both cells perform the function of food supply. Glycogen from the digestive system enters cells of the connective tissue penetrated by the gonad and from there the gonad (Bayne, et al., 1975; Gormosova, Shapiro, 1984). In some mollusks, the adductor functions as a glycogen and protein depot which is important for oogenesis (Barber, Blake, 1985). In *Glycymeris glycymeris*, all muscular tissues participate in collection of glycogen which serves as a source of energy for vitellogenesis. In turn, resorption products of unshed oocytes are used for somatic development. According to Galap et al. (1977), *G. glycymeris* can be placed in the K-strategy group based on these considerations.

After spawning or during resorption of gametes outside the reproductive season, the orderly pattern of the ovary is disturbed and gametes are phagocytosed with accessory cells of the gonad and also cells of the connective tissue invading the gonad. The acinus structure is reconstructed with commencement of gametogenesis. Details of the transfer of nutrients to oocytes of bivalves are not known.

Sea cucumbers. Based on imcomplete and indirect data of other investigators (Atwood, 1973a; Krishnan, Dale, 1975; Green, 1978) Walker (1982) concluded that significant differences occur in the spatial organization of gametogenesis of sea cucumbers compared to the corresponding phenomena in sea stars. Our data, on the contrary, suggest a common sturcture of anici in all three classes of echinoderms studied by us. Significant differences were detected, as expected, in the structure of the gonad wall of sea cucumbers. Moreover, male and female gonads of sea cucumbers are characterized by very deep evagination of the hemal sinus in the cavity of tubules.

Ciliated follicular cells surrounding oocytes make up the internal structure of the ovarian acinus in *Stichopus japonicus*. They have a flattened body with an extended nucleus and long lamellopodia. Microvilli are clearly seen, at least in some cases, at the border of two follicular cells adjoining the acinus wall. It is possible that nutrient transport from the hemal sinus to the oocyte occurs here. 2,8-disubstituted adenine responsible for the maturation of oocytes in sea cucumbers is probably produced by these cells (Smiley, 1987, 1988). Follicular cells of adjacent oocytes closely adher to one other.

Follicular epithelium surrounding the oocyte transforms in the areas where oocytes are absent into parietal epithelium lining the tubule wall. In the zone of the oocytes adjoining the tubule wall, the thickened basal membrane of the oocyte, oolamina, is found. It forms a barrier between

the hemal sinus and subfollicular space surrounding the oocytes (Smiley, Cloney, 1985).

Besides follicular cells, the ovary contains accessory cells attached to the acinus wall. The cytoplasm of accessory cells is filled with phagosomes and forms filopodia.

The acinus wall of the testes has a structure similar to that of the ovarian acinus wall. The internal structure of the acinus of the testes is made up of gigantic axial cells surrounded by spermatogenic cells. Processes and lacunae of the hemal sinus of the gonad are invaginated deeply into the axial cell and only a narrow strip of cytoplasm of the axial cell between the space of the hemal sinus and spermatogenic cells remains. This creates an optical impression of the absence of typical spermatogenic columns. The nucleus of the axial cell is situated apically; its cytoplasm spreads to the center of the acinus in the form of lamellopodia and filopodia. The nucleus has an irregular ovate extended form. The cytoplasm contains various electron-dense granules and phagosomes. In some cases, phagocytosed sperm cells are seen. The axial cell is surrounded on all sides by spermatocytes and spermatids contacting processes or body of the axial cell. Toward the acinus wall, the axial cell narrows and changes into a narrow stalk accompanied by spermatocytes. On contact with the acinus wall, the stalk of the axial cell forms a flattened base extending along the wall with spermatogenic cells set on it. The base of the axial cell connects with the basal membrane of the hemal sinus (Drozdov et al., 1986).

Nutrients enter the gametocytes of sea cucumbers probably from the hemal sinus. The cells of the gonad wall of *Cucumaria frondosa* contain abundant polysaccharide and protein granules. Krishnan and Dale (1975), however, detected no changes in the granules of these cells during gametogenesis. Without going into a description of the transport of nutrients into oocytes of sea cucumbers, it may be pointed out that the cells of the peritoneal lining of the ovary of sea cucumber *E. fraudatrix* filled with granules, judging from electronograms, are present in a state of apocrine secretion and discharge the content through the basal membrane into the hemal sinus of the gonad. Ingestion of nutrients from the coelomic fluid and their transfer to the hemal sinus of the gonad by peritoneal cells of the gonad has been suggested on the basis of results of electron microscopic analysis of the structure of the ovary wall of *Stichopus californicus* (Smiley, Cloney, 1985).

Sea stars. In the testes of sea stars *Ctenodiscus crispatus, Hippasteria phrygiana,* and *Asterias vulgaris,* spermatogenic epithelium is divided into numerous columns. Each fully developed column consists of one or more axial somatic cells surrounded by roughly 400 spermatocytes (Walker, 1982; Walker, Larochelle, 1984). Processes of gametes pass along the extended surface of axial cells and reach the base of columns lying on the inner

wall of the hemal sinus. Processes of gametocytes contain endocytic vesicles, and nutrients probably reach here from the hemal sinus into gametocytes (Walker, 1979). Spermatocytes move from the base of columns along axial cells to their tips. Spermatogonia begin mitotic division only after contact with the axial cell is disturbed. Later, while moving along the spermatogenic column, spermatocytes become competent for meiosis. In this period, they pass through the early prophase of meiosis and complete meiotic division after leaving the spermatogenic, column (Walker, Larochelle, 1984). Upon completion of differentiation of spermatocytes and spermatids, the column is destroyed. Spawning occurs later and is followed by the agametogenic phase of the gonadal cycle is which columns are lacking. Unreleased spermatozoa as well as spermatids and spermatocytes are phagocytized by so-called vesicular cells (Cognetti, Delavault, 1962) which represent modified axial cells. On the other hand, these very cells secrete steroids. Probably, as in mammals, molecules absorbed during phagocytosis are later used for steroid synthesis. Under the influence of external factors, steroids emerge from "vesicular cells" of the testis of *Asterias rubens* into the genital hemal sinus, from there into the circulatory system of the pyloric ceca (Cuenot, 1948; Walker, 1974), and stimulate the transfer of nutrients from the ceca to the gonad (Schoenmakers, 1980). It may be pointed out in this context that the presence of special organs storing nutrients for gametogenesis and other processes moderates seasonal and abrupt fluctuations of feeding conditions and enables the spread of energy supply for reproduction throughout the year. This is an important aspect for irregularly feeding predators such as sea stars.

Kubota et al., (1977) described cells which synthesize l-methyladenine in testes of sea star *Patiria pectinifera.* This compound controls maturation of spermatocytes and spermiation. These cells contain phagosomes with sperm cells and probably belong to the same cell type as axial cells.

On the whole, the spatial organization of spermatogenesis in sea stars (in echinoderms in general) is highly similar to the organization of spermatogenesis in vertebrates (Gabaeva, 1982, 1984; Simpson, Poccia, 1987).

In ovarian acini, spatial relationships between gametes and somatic cells are somewhat converse to the relationships observed in the testes. Somatic cells—homologues of axial cells of spermatogenic columella—surround the growing oocytes and form a layer of follicular epithelium which envelops the oocyte except the zone of its contact with the basal membrane of the hemal sinus and, later, after the oocyte is dislodged from the wall, somatic cells wholly surround it. Oocytes near the wall zone receive nutrients from the hemal sinus and engulf them by endocytosis (Beijnink et al., 1984). Oocytes dislodged from the wall receive nutrients from the surrounding space, reaching there from the hemal sinus or from phagocytizing cells. In some species of sea stars producing

large eggs—*Asterina gibbosa, Leptasterias tenera, Benthopecten simplex*, and others—the nutrient source directly enters the gonad and forms there the so-called vesicular phagocytic tissue (Cognetti, Delavault, 1962; Worley et al., 1977; Pain et al., 1982) but the accumulation of nutrients for gametogenesis in pyloric ceca is not so obvious. We found a very similar phagocytic tissue in *Henricia hayashi*. Nutrients reach these cells, particularly as a result of phagocytosis of oocytes which have not attained a definitive size and thus perform the role of nutrients to eggs, for example in *Bathibiaster vexillifera* (Tyler et al., 1982). In other words, shunting of food chains arises in such cases. Cells organizing microcompartments of the acinus concomitantly serve as secreting cells producing steroids—estrogen and progesterone—which control vitellogenesis (Voogt et al., 1984; Voogt, 1987) and 1-methyladenine, which controls maturation of oocytes, ovulation and shedding (Chaet, 1966; Schuetz, 1971; Cochran, Kanatani, 1975; Kanatani, 1975, 1984; Mita, 1991). After spawning, the structure of the acinus is destroyed and accessory cells phagocytize the unspawned late oocytes and very early gametocytes.

Sea urchins. According to Ch. W. Walker (1982), "leaving aside the dimensions and undoubted function of the accumulation of nutrients, the significant similarity cannot be ignored between accessory cells in testes of sea urchins and axial cells in spermatogenic columns of sea stars". In fact, in heart urchin *Echinocardium cordatum*, for exmaple, the internal structure of the testis, according to Caullery (1925), is formed of a double row of accessory cells perpendicular to the acinus wall. Rows of spermatogenic columns are in contact with the above rows of cells. After the completion of spermatogenesis and before spawning, this structure is destroyed and the acinus is filled with spermatozoa.

Unlike in sea stars, nutrients do not accumulate in the genital hemal sinus of sea urchins but, before commencement of gametogenesis enter the accessory cells, predominantly as glycogen and glycoproteins (Zalutskaya et al., 1986). Accumulation of nutrients in accessory cells to meet the requirement of gametogenesis was reported as early as 1877 by Giard (1877; cited from Caullery, 1925). In this respect, sea urchins stand apart from other echinoderms and resemble sea stars with lecithotrophic larva.

The main component of accessory cells in both sexes, glycoprotein, is the result of expression of a unique vitellogenic gene (Shyu et al., 1987); this glocoprotein discharged from the accessory cells, during gametogenesis enters the oocytes while its fate in spermatogenic cells is not clear (Unima et al., 1998). The transfer of nutrients from accessory to spermatogenic cells has not been described. After spawning, accessory cells equipped with flagella are transformed into phagocytes (Beig, Cruz-Landim, 1975).

Groups of oogonia are seen in the ovaries of sea urchins between accessory cells attached to the gonad wall. At commencement of the gametogenic period, acinus is almost entirely filled with accessory cells. In ovarian sections of sea urchin *Strongylocentrotus nudus*, accessory cells covered an area of 77% after spawning but only 5% before spawning, of the total area of the acinus section (Varaksina, 1985). According to Caullery (1911, 1925), who investigated the gonadal cycle in *Echinocardium cordatum*, accessory cells seen after spawning in the periphery of the acinus represent a new generation of cells. These cells vary in size on average from 30 to 50 μm and nuclei from 3 to 5 μm. Accessory cells may form numerous fine outgrowths or filopodia; boundaries between cells are poorly discernible and may create an impression of a single multinuclear syncytium in optical preparations. Many globules are usually present in accessory cells or a large vacuole (Holland, Giese, 1965; Varaksina, 1978). Nicotra and Serafino (1998) studied the dynamics of the ultrastructure of accessory cells of testes in sea urchin *Paracentrotus lividus*.

In *Anthocidaris crassipina* and *Hemicentrotus pulcherrimus*, the growing oocytes are surrounded by processes of accessory cells (Masuda, Dan, 1977). As a result, a follicular formation arises which, in our view, differs from a typical follicle (for example, of sea stars) in that the oocyte is surrounded not by cellular bodies, but their processes, while their bodies lie in the acinar lumen or adjoin its wall. Thus, it cannot be surmised that oocytes in ovaries of sea urchins lack a follicular cover; its role is performed by processes of accessory cells. In some sea urchins of order Spatangoida, oocytes are surrounded by a "standard" follicular cover formed by follicular cell bodies; further, gigantic accessory cells, characteristic of sea urchins, are lacking in them (Dzyuba, 1978; Harvey, Gage, 1984).

During vitellogenesis, oocytes in *Hemicentrotus pulcherrimus* form microvilli through which nutrients probably pass from the microenvironment of the oocyte having reached there from accessory cells (Takashima, Takashima, 1965; Takashima et al., 1978) or directly from the hemal sinus. Ozaki (1982) demonstrated the biochemical and immunological similarity of glycoproteins of the egg yolk in sea urchins with glycoproteins of accessory cells and coelomocytes, assuming that nutrients synthesized in (or entering—VLK) coelomocytes enter through the coelom or, bypassing it, the accessory cells of the ovary and later oocytes. Cells of the ovary (Ozaki et al., 1986) and intestine (Shyu et al., 1986) synthesize yolk protein precursors but coelomocytes from the perivisceral coelom serve as the main source of all yolk glycoproteins (Harrington, Ozaki, 1986). Coelomic fluid of sea urchins contains a large amount of yolk protein precursors (Giga, Ikai, 1985a, b; Shyu et al., 1986). According to Aizenshtadt (1984), accessory cells may particiate only in the transfer of low-molecular substances; hence she assigned to them, as did Chatlynne (1969), mainly the role of phagocytes. These cells, however,

accumulate nutrients (for transferring to gametes) not only in the course of resorption processes, but also when processes of phagocytosis of gametes are not taking place in the gonad. It must be pointed out that the material of phagocytized eggs and oocytes in not the main but only an additional source of nutrient supply to accessory cells of the ovary.

The converse relationship noticed in ovaries of sea urchins between bodies occupied by accessory cells and gametes is easily explained by the transfer of substances from accessory cells to gametes (see also Holland, Holland, 1969; M.M. Walker, 1982). Accessory cells of ovaries and testes in sea urchins contain 1-methyladenine but, unlike sea stars in which 1-methyladenine is present in the gonad only before spawning, this substance is contained in the gonads of sea urchins probably at all times or almost so (Kanatani, 1975). A detailed analysis of the mechanisms of maturation of germ cells and spawning was done by Giese and Kanatani (1987) whose investigations over many years have established the course of studies in this field.

Brittle stars. In the ovaries, late vitellogenic oocytes are firmly attached to germinative epithelium by a complex consisting of specialized cells and intracellular microtubules located between the oocyte membrane and nucleus (Moloney, Byrne, 1994); Selvakumaraswamy, Byrne, 1995; Stewart, Mladenov, 1995). At the base of mature gonads are miniature testes and ovaries containing cells in early stages of gametogenesis; subsquently, these gonads replace the former. As already pointed out, a similar pattern has been recorded for sea cucumbers (Smiley 1988). As in other echinoderms, follicular oogenesis and linkage of growing germ cells with the hemal sinus have been observed in brittle stars (Byrne, 1997). The hemal sinus in testes of brittle stars projects into the center of spermatogenic styles, probably performing the feeding function as in the course of oogenesis.

Gametogenesis

Eckelbarger (1994) pointed out that evolutionists who argue the semelparous or iteroparous reproduction, species undergoing r- or K-strategy, the importance of interspecific differences in egg size, energy content in them and, as a consequence, type of larva, should also examine the role of oogenesis since the courses of development established during this process directly influence the later life cycles.

In the context of the problem of reproductive strategy, let us briefly study four gametogenic processes—gonial divisions in oogenesis and spermatogenesis, accumulation of yolk and RNA in oogenesis, formation of cyto- and karyoskeleton in gametes, as well as processes of degeneration and resorption of gametes. Animals with different reproductive strategies may differ significantly in intensity of these processes.

Gonial divisions

Gonial divisions and spermatogenic cycles have been studied in the testes of bivalves and echinoderms by several investigators (Holland, Giese, 1965; Kosenko, 1975; Yamashita, Iwata, 1983). Numerous spermatogonial mitoses were seen while describing gonadal cycles in the species studied by us (Kasyanov et al., 1980; Kasyanov, Kornienko 1984).

Gonial divisions in ovaries have been detected by some investigators (in particular, Brusle, 1970) and controversial literature published about the origin of oogonia in mollusks and echinoderms. Some researchers consider it possible that oogonia originate from dividing somatic cells of the gonad wall (Tennent, Ito, 1941; Gnezdilova, 1971; Dzyuba, 1971). It has been shown however, that there is only one way of replenishing the stock of gametes in mollusks and echinoderms and that is by gonial divisions of primary oogonia (Holland, Giese, 1965; Piatigorsky, 1974; Dzyuba, Maslennikova, 1982b; Novikova, 1982).

In order to ensure a given type of reproductive strategy or tactics, control of gonial divisions is of great importance. Control mechanisms have not been well studied but it is clear that gonia invariably present in the ovary and testes serve as points of application of control and form a unique source for supplementing the germ cell pool. It has been shown that cerebropleural ganglia in bivalves produce a hormone which stimulates mitosis and causes gonial division (Houtteville, Lubet, 1974L). This hormone in *Mytilus edulis* is proteinic and present in the hemolymph of the mollusk, probably en route to target cells (Mathieu et al., 1988). There is no doubt that endocrine control of gonial divisions is a constituent part of the control of the entire gonadal cycle. The role of polyamines as regulators of gonial divisions in gonads of echinoderms has been revealed (Asotra et al., 1987).

Vitellogenesis

If the number of eggs produced by a female is determined primarily by the intensity of oogonial divisions, the amount of nutrient reserves in each egg depends on the intensity and duration of vitellogenesis. In a review of the diversity of vitellogenic mechanisms in multicellular animals, Eckelbarger (1994) stated that the so-called opportunistic species evolved special mechanisms of vitellogenesis for rapid conversion of the ingested food into eggs while many other species (for example, those spawning once a year) use slower mechanisms of vitellogenesis. Complex relations prevail between habitat, food, food strategy, digestive limitations, and mechanisms of vitellogenesis which should be taken into consideration for a total understanding of the dynamics of marine communities.

Wourms (1987) analyzed the mechanism of yolk formation in different groups of marine invertebrates. In animals with different reproductive

strategies, not only the quantity of yolk granules in the egg, but also the ultrastructure and biochemical composition of granules differ. In the context of this situation, it may be pointed out that lipids are characteristic of the egg yolk of species with lecithotrophic strategy; lipids are more economic from the energy point of view than proteins and carbohydrates and comprise a significant part of the egg yolk of species with planktotrophic strategy (Kaufman, 1976, Lawrence et al., 1984).

Bivalves. In *Anadonta,* yolk granules are formed from vesicles which represent precursors of granules in the region of the Golgi apparatus (Beams, Sekhon, 1966). According to Beams and Sekhon, these vesicles—precursors—are formed by pinocytosis as well as endogenously. Similar conclusions were drawn in investigations on vitellogenesis in *Ostrea cucullata* (Lin, Quang, 1983). The first granules representing yolk precursors in oocytes of *Spisula solidissima, Mytilus edulis,* and *Brachidontes virgilia* are formed in the region of the so-called yolk nucleus which consists of cisterns of granular endoplasmic *reticulum,* porous plates and mitochondria (Rebhun, 1956; Reverberi, 1966; Bernard et al., 1988). It has been suggested that at commencement of the gametogene cycle, vitellogenesis in *Mytilus edulis* proceeds by heterosynthesis with pinocytosis by oocytes of nutrients from mantle storage cells. In later stages of gametogenesis, yolk is formed by autosynthesis using up the amino acid pool formed in oocytes in the preceding processes of intense proteolysis in mantle cells (Pipe, 1987a, b; Peck, Gabbott, 1990).

In bivalve mollusks, there are differences in size and composition of yolk granules of oocytes which depend on egg size and nature of development. In mollusks with large eggs (*Yoldia hyperborea, Portlandia arctica, Nuculana pernula, Musculus laevigatus, M. discors,* and others), yolk granules may measure 9 μm and contain a signficant amount of lipoproteins. In bivalves with small eggs (*Mytilus edulis, Modiolus modiolus, Hiatella arctica, Mya arenaria,* and others), yolk granules are smaller in size with a lower content of lipoproteins (Kaufman, 1977).

Sea cucumbers. In *Thyone briareus,* yolk is formed during the interaction of the endoplasmic reticulum and Golgi apparatus; endogenous yolk formation has been suggested (Kessel, 1966). Exogenous type yolk protein enters oocytes of sea cucumbers *Stichopus californicus* from the hemal sinus through long microvilli into the vegetal pole of the oocyte (Smiley, 1988). In this same work, Smiley cites a communication from Eckelbarger that in sea cucumbers with eggs of large diameter, unlike in *S. californicus* material inflow into the oocyte proceeds throughout all its surface.

In sea cucumbers with small eggs, yolk granules about 2 μm diam have a simple granular structure while in those with large eggs, some granules are larger, about 5 μm diam and contain homogeneous lipid inclusions (Lönning, 1976).

Sea stars. In oocytes of *Asterias rubens,* yolk is associated with the Golgi apparatus (Harvey, 1931). In oocytes of *Asterina gibbosa,* part of the inclusions of nutrient reserves is in contact with dictyosomes of the Golgi apparatus (Delavault et al., 1965). In *Asterias amurensis* and *Patiria pectinifera,* development of yolk granules is associated with dictyosomes of the Golgi apparatus (Novikova, 1982). In the latter species (and probably in other sea stars as well), vitelline proteins are synthesized in the endoplasmic reticulum; they are converted into yolk granules in the Golgi apparatus by combining with lipids and carbohydrates (Aizenshtadt, Vasetskii, 1986). Beijnink and his colleagues (1984) left the question of auto- or heterosynthetic formation of yolk in sea stars open and showed that the stem connecting the growing oocyte with the basal membrane of the hemal sinus serves as a site for accumulation of granules—yolk precursors—in *Asterias rubens.*

Lönning (1976) pointed out that in sea stars with small eggs and planktotrophic larva, yolk granules of oocytes are about 2 μm diam, surrounded by a membrane, and have a complex internal structure; the structure of large (4 μm) yolk granules of oocytes in sea stars with large eggs and lecithotrophic larva is simpler. Kaufman (1977) in his study on gametogenesis of sea stars with different types of development showed that lipid inclusions comprise a large proportion of nutrient reserves of oocytes in sea stars with lecithotrophic larvae or direct development and large eggs; in sea stars with planktotrophic larvae and small eggs, lipid inclusions are few. Our data on the ultrastructure of oocytes is *Distolasterias nipon* and *Henricia hayashi* also point to differences in the structure of yolk granules in sea stars with different types of development. Yolk granules of oocytes in *D. nipon* are fewer than in *H. hayashi* and have a different, fine-grained structure.

Sea urchins. In *Arbacia punctulata,* development of the Golgi apparatus and rough endoplasmic reticulum precedes accumulation of yolk and cortical granules (Bal et al., 1968). During oogenesis the amount of ribosome increases and processes of synthesis of yolk precursors take up much of the growth period; the vitellogenic process *per se* proceeds very rapidly (Verhey, Moyer, 1967). According to the data of Tominaga and his colleagues (1978), yolk in the oocytes in *Hemicentrotus pulcherrimus* is not only of endogenous but also exogenous origin. According to Anderson (1974), yolk in the oocytes of *Arbacia punctulata* is formed only by autosynthesis. Recent studies confirm that accessory cells as well as oocytes of sea urchins may synthesize some yolk glycoproteins (Ozaki et al., 1986; Shyu et al., 1986). The question of whether yolk is produced by auto- or heterosynthesis is not very important, however, since in any case the basic ingredients for vitellogenesis come from outside and the only differences are extent of completion of yolk formation and the

possibility of its entry or the entry of its precursors into the oocyte by diffusion or pinocytosis. Japanese investigators emphasize pinocytosis, assuming that lipids and glycogen penetrate the oocyte in this manner (Takashima, Takashima, 1965). It is possible that the heterosynthetic manner of yolk formation, as in other groups of animals, is characteristic of species with a large yolk content in eggs (Calow, 1977)

In sea urchins with small eggs, yolk granules 1-1.5 μm diam possess a coarse internal structure made up of densely packed granules. In sea urchins with large eggs, yolk granules 3-4 μm diam contain inclusions with a homogeneous content resembling lipid globules (Lönning, 1976). In fact, *Heliocidaris erythrogramma*, sea urchin with direct development, has yolk granules differing by their structure and protein composition from typical yolk granules of sea urchins with larvae (Scott et al., 1990).

Accumulation of messenger and ribosomal RNA and morphological changes in nucleolus

When nutrient reserves in the egg are large, the rate of synthetic processes in embryo cells is restricted by the possibilities of the protein-synthesizing system. Important elements of this system are the messenger RNA (mRNA) and ribosomal RNA (rRNA) synthesized in nucleoli. Accumulation of mRNA in oogenesis is perhaps a universal feature of any egg. In sea urchin eggs, after fertilization maternal mRNA enters the composition of polyribosomes and accounts for 2-4% of the entire RNA in the egg (Brandhorst, 1985). In oocytes of echinoderms, RNA (probably mRNA) is localized in the so-called heavy bodies; in oocytes of bivalves, localization occurs in the so-called yolk nucleus. After fertilization, high RNA concentrations are seen in the polar lobes of bivalve eggs (Jeffery, 1983).

The diverse patterns of functioning of nucleoli in the oogenesis of animals with different reproductive strategies revealed by morphological methods, reflect the differences in production intensity of rRNA stored for protein synthesis in the embryo cells (Aizenshtadt, 1984).

Bivalves. A fivefold amplification of rRNA cistrons was recorded in oocytes of *Spisula solidissima* (Brown, David, 1968). A small extracopying of rDNA was found in *Mulinia lateralis* and *Mytilus edulis* (Kidder, 1976). True multiple nucleoli have not been detected in bivalves irrespective of the nature of their oogenesis and subsquent development. In *Portlandia arctica* the content of the large nucleolus enters the caryoplasm before vitellogenesis with separation of some small nucleolus-like bodies; in *Yoldia hyperborea*, the main nucleolus cleaves into small bodies during vitellogenesis while the nucleolus of the oocyte in *Musculus laevigatus*, divides into 1 or 2 small nucleoli in the course of vitellogenesis. Similarly, in *Astarte borealis*, *A. elliptica*, and *A. montagui*, 2 or 3 additional nucleoli bud from the main nucleolus during vitellogenesis; in many oocytes, the

nucleolus fragments (Kaufman, 1977). Development in the aforesaid species is either direct or with lecithotrophic larvae. However, it is not always clear whether these pictures reflect true division or budding of effective nucleoli or, rather, the result of fragmentation of degenerating nucleoli.

In the oocytes of other species investigated, viz. *Mytilus edulis*, *Modiolus modiolus*, *Macoma balthica*, and others, Kaufman (1977) observed neither divisions nor budding of nucleolus into secondary formations but noted separation of fragments and small grains from the nucleolus during vitellogenesis. In this group, development proceeds with or without planktotrophic larvae. Thus, differences are possible in the functioning of the main nucleolus in bivalves with different types of development.

For species of bivalves with small eggs (up to 65 μm) and planktotrophic larvae investigated by us, secondary nucleoli are not typical in oocytes. Eggs are large in *Callista brevisiphonata* (about 130 μm) and *Glycymeris yessoensis* (about 120 μm); the nuclei of oocytes in these species have a very large main nucleolus and some secondary ones or nucleolus-like bodies. Development of these species has not been studied.

Sea cucumbers. Nuclei of oocytes in *Thyone briareus* contain many nucleoli: central ones with the usual nucleolonema and peripheral flattened ones in contact with the nuclear membrane and supplying material to the cytoplasm, especially at commencement of oocyte development and commencement of maturation (Kessel, 1966). In *Eupentacta fraudatrix*, lampbrush chromosomes and numerous nucleoli formed at commencement of the diplotene stage in chromosomes are found near the nuclear membrane. As oocyte development progresses, these formations are disposed on the inside of the nuclear membrane. In this species, at commencement of the diplotene stage, not one but 20-30 nucleoli arise all at once. These nucleoli are vacuolized and contain RNA and DNA (Nizovskaya, Arronet, 1975). Lampbrush chromosomes, later occupying a position near the nuclear membrane and numerous marginal nucleoli, up to 25, are also distinctly discernible in *Cucumaria frondosa* (Arronet, 1971). The number of nucleoli increases in the course of oogenesis in *Holothuria tubulosa* as well (Günther, 1904). A single nucleolus growing in the course of oogenesis together with greater RNA content is clearly seen in oocytes of *Stichopus japonicus*. One or two spherical bodies separate from the nucleolus and move toward the nuclear membrane and disappear in its vicinity (Nizovskaya, Arronet, 1975). In sea cucumber *Chirodota laevis*, the oocyte contains 1 or 2 nucleoli with numerous vacuoles discharging the content into karyo- and later into cytoplasm (Kaufman, 1977). The latter two species have planktotrophic larvae and the earlier ones lecithotrophic. Thus, in sea cucumbers with lecithotrophic larvae, many nucleoli are formed during oogensis while in cucumbers with planktotrophic larvae, only 1 or 2 nucleoli are formed in the oocyte.

Sea urchins. The oocyte nucleus in *Arbacia punctulata* contains a single nucleolus including labeled uridine from the diplotene stage (Bal et al., 1969). The amplification level of rRNA cistrons in oocytes of sea urchins is probably not high (Bal et al., 1968; Enesco, Man, 1974).

According to the data of Afzelius (1957), one main and a few secondary nucleoli stained by toluidine are present in the oocyte nuclei of different species of sea urchins. The oocytes of *Strongylocentrotus droebachiensis* contain a single nucleous (Kaufman, 1977). One large nucleolus was detected in oocyte nuclei of deepwater sea urchin *Pourtalesia heptneri* (Dzyuba, 1978) and brooding Antarctic *Abatus cordatus* (Magniez, 1983). The same picture was observed by us in oocytes of sea urchin *Asthenosoma ijimai* which develops with lecithotrophic larvae.

Thus, oocytes of sea urchins are characterized by a single nucleolus; most species studied have planktotrophic larvae. Oocytes of species from the Sea of Japan studied by us contain 1 or 2 nucleoli.

Sea stars. Amplification of rRNA cistrons in uninucleolate oocytes of *Asterias forbesi* has not been observed (Vincent et al., 1969).

Species in which essentially a single nucleolus functions in oogenesis include both those with planktotrophic larvae and lecithotrophic larvae, among latters *Leptasterias hexactis* (Chia, 1968b) and *Asterina gibbosa* (Delavault et al., 1965). In general, oocytes of most species of sea stars investigated contain a single main nucleolus, accompanied sometimes by 1-3 additional ones (Kaufman, 1977; Novikova, 1982). However, Jordan (1910) paid attention to the fact that oocyte nuclei in *Henricia sanguinolenta*, like oocyte nuclei of other sea stars of the same family—*Echinaster crassispina* (Jordan, 1908)—form numerous nucleoli. Chia (1970) drew attention once again to this feature of oogenesis in *Henricia*. He showed that numerous nucleoli form as a result of budding of a single large nucleolus but did not find RNA synthesis in nucleoli on autoradiographic analysis of inclusions of ^{3}H-uridine in oocytes.

Lampbrush chromosomes were detected for the first time among sea stars in *Echinaster sepositus* (Delobel, 1971). Chromosomes of this type are also present in *Henricia hayashi* inhabiting the Sea of Japan. In this species, depending on the state of the nucleolar apparatus, some stages of oocyte development in the vegetative phase can be differentiated. These are successively characterized by : a presence of a single large body containing rDNA in chromosomes; b) formation of primary chromosomal nucleolar complex; c) manifestation of secondary extrachromosomal nucleolar complexes; d) formation of extrachromosomal multiple nucleoli; and e) cessation of division and degradation of secondary nucleoli. The process of multiplication of nucleoli by the cascade mechanism leads to an immense increase in their material content, especially DNA. Transformation of the nucleolar apparatus described above justify the

assumption that amplification of the nucleolar organizer occurs in the oocytes of *Henricia* species (Gaginskaya, Kasyanov, 1983; Gaginskaya et al., 1983, 1987). The morphology of this process is evidently similar in all members of family Echinasteridae investigated (Jordan, 1908, 1910; Chia, 1970; Kaufman, 1977).

The content of ribosomal genes in nucleolar complexes and oocyte nucleoli in *H. hayashi* was established by the method of hybridization of nucleic acids (DNA/DNA) in preparations. Ribosome clones 18S and 28S of *Drosophila melanogaster* genes used as standards were laid on sections of *Henricia* ovaries glued to a slide glass. Chromosomal as well as extrachromosomal nucleoli and nucleolar complexes produced a high level of labeling on radioautographs after hybridization with ^{3}H-rDNA of *Drosophila*. Localization of label on radioautographs in most cases coincides with the distribution of a dense fibrillar component in the nucleoli (Gaginskaya et al., 1984, 1987).

Formation of numerous nucleoli and large amounts of extrachromosomal DNA is generally uncharacteristic of echinoderm oocytes. Numerous marginal nucleoli were described in growing oocytes of sea cucumbers *Cucumaria frondosa* and *Eupentacta fraudatrix* (Arronet, 1971; Nizovskaya, Arronet, 1975) but there is no proof of DNA amplification since all nucleoli in oocytes of these animals are formed on chromosomes and do not lose contact with them on prolonged oocyte development. Kessel (1966) detected marginal nucleoli in oocytes of sea cucumber *Thyone briareus* and brittle star *Ophioderma panamensis* but the nature of these nucleoli is not clear.

Thus, oocytes of all the bivalve species studied to date are characterized by a single principle nucleolus, but in species with lecithotrophic strategy, it has larger dimensions and undergoes fragmentation in late stages of vitellogenesis, reflecting perhaps its heightened activity. A similar picture is noticed in sea urchins. In sea urchins with planktotrophic strategy, the oocyte has 1 or 2 nucleoli. Oocytes of sea cucumbers with lecithotrophic strategy contain numerous marginal nucleoli which are probably formed by numerous nucleolar organizers. In sea stars with planktotrophic strategy, RNA cistrons are not amplified and one long-lasting large nucleolus functions. In sea stars with lecithotrophic strategy, a cascade mechanism of amplification of ribosomal genes occurs, leading to formation of numerous extrachromosomal nucleoli with high DNA content.

Cyto- and karyoskeleton of gametes

Sea stars. The distribution of fibrillar actin was investigated in oocytes and spermatozoa of sea stars *Aphelasterias japonica* and *Henricia* sp. (*hayashi*) characterized by planktotrophic and lecithotrophic types of development

respectively. In oocytes of *A. japonica* (about 100 μm diam), the concentration of fibrillar actin, the main protein of cyto- and karyoskeleton, is maximum in a thin cortical layer of ooplasm as well as in the nucleolus. Large (up to 900 μm diam) oocytes of *H.* sp. are highly rich in fibrillar actin localized predominantly in a thick layer of cortical ooplasm and in the karyoplasm. A large amount of fibrillar actin in the karyoplasm renders its detection difficult in many nucleoli of oocytes of *H.* sp. Probably, fibrillar actin of cytomatrix performs not only a supportive, but also a regulatory function during gametogenesis and subsequent embryogenesis (Isaeva, 1994). In very large spermatozoa of *H.* sp., the concentration of fibrillar actin in the zone of the acrosome is more than in the acrosome of spermatozoa of *A. japonica* (Isaeva, Kasyanov, 1998).

Sea urchins. In spermatids of sea urchins with indirect development, *Salmaris bicolor* and *Diadema setosum*, the flagellum is formed by two methods. In most cases the basal body of the flagellum and later the flagellum itself, is located perpendicular to the cell membrane of the spermatid as usual; in 30% cases, the basal body lies parallel to the cell membrane and the axoneme is initially developed without extrusion from the spermatid body and a spermatozoon with upward flagellum is formed later (Au et al., 1998). These observations together with the data of these authors on the diversity of spermatid formation in another sea urchin, *Anthocidaris crassispina*, (Au et al., 1998) may be interpreted as inevitable "interruptions" in the work of the highly productive, fast conveyor-like system of production of spermatozoa in animals with planktotrophic larval strategy.

Being at the very beginning of data accumulation on gamete cyto- and karyoskeleton we assume significant role of these organelles in creation of pre requisites for planktotrophic or lecithotrophic strategies.

Degeneration and resorption of gametes

Having analyzed the cytological mechanisms responsible for various types of reproductive strategies following gametogenesis, processes of degeneration and resorption in the gonad need to be studied. As investigations to date are few, these aspects are presented for bivalves and echinoderms together.

Resorption of unreleased gametes and other cells of the gametogenic series were first described in echinoderms by Caullery (1911, 1925), who noted certain details. First, the gonad cavity is cleared of gametes of the preceding population and thus space made for a new gametogenic cycle. Second, nutrients accumulated in the resorbed gametes and comprising an additional source of material and energy for the growing gametes (in some cases even for the entire organism) are recycled. Third, products of resorption of gametes may form a source for the synthesis of hormonal

substances produced by the gonad. Lastly, some investigators have suggested that degeneration and resorption of gametes initiated under the influence of endogenous and exogenous factors of neurosecretory system, in turn, represent a regulator of gametogenic events. Proliferation of gametes of the next generation cannot commence (or is delayed) without resorption and degeneration of unshed mature gametes.

Thus, resorption is a very important process in the gonad—a process which in some periods of the gonadal cycle is definitive (Caullery, 1911, 1925; Fuji, 1960b). While processes of gametogenesis are markedly conservative and stable against interferences, processes of autolysis, degeneration, and resorption of gametes are more labile and largely subject to control by external factors. Lability of autolysis, degeneration and resorption processes of gametes is distinctly manifest when the animal is exposed to deleterious, including anthropogenic, factors. High concentrations of metals and other pollutants in water lead to the activation of lysosome systems of cells and development of inflammatory processes, as a result of which gametes undergo autolysis and granular hemocytes invade the gonads (Sunila, 1984; Moore et al., 1987; Lowe, 1988; Pipe, Da Silveira, 1989). An important function of resorption is probably control of fecundity in response to changing environmental conditions (Holland, Giese, 1965; Chatlynne, 1969; Yamashita, Iwata, 1983; Motavkin, Varaksin, 1989). It is known that under unfavorable conditions, autolytic and resorption processes in gonads of bivalves and echinoderms may be so strongly manifest that almost all gametes are resorbed and the animal does not spawn (Nizovskaya, 1971; Bayne et al., 1975). In gonads of sea stars, autolysis and subsequent resorption of small-size oocytes are observable during completion of the growth period in most oocytes. This promotes completion of vitellogenesis in the leading size group of gametes (Pearse, 1965; Worley et al., 1977; Tyler, Pain, 1982a, b).

A good example of the "strategic" application of resorption processes is development of so-called phagocytic tissue in sea stars changing over to development with lecithotrophic larvae (Brusle, 1970). Gonads of such sea stars are characterized by the constant presence of a considerable number of accessory cells which intensely resorb numerous gametes that have not completed gametogenesis or not been released after spawning (Pain et al., 1982; of Ch. W. Walker, 1982). Tyler and Pain (1982b), having analyzed the degree of development of accessory cells in gonads of deepwater sea stars, noted the parallel course of evolution of phagocytic (according to Brusle, 1970) tissue in gonads. In Benthopectinidae, numerous accessory cells closely adjoin oocytes and phagocytize the unreleased gametes; in Astropectinidae, unreleased oocytes undergo autolysis while accessory cells resorb small oocytes (less than 400 μm). It is possible that resorption products pass into oocytes which attain maximum (about 1000 μm) size (Tyler et al., 1982); in Goniasteridae,

accessory cells form a reticulum around the oocyte and sometimes perform the role of phagocytes.

It must be mentioned that in sea stars with considerably developed accessory cells, the cycle of accumulation and release of nutrients in pyloric ceca, followed by their utilization by the gonad, in manifest to a lesser extent than in sea stars with poor development of phagocytic tissue (Ch. W. Walker, 1982). Among the wonders of nature is the feeding by degenerating unfertilized egg cells of pentacula of sea cucumber *Leptocynapta clarki* developing after fertilization within the ovary (Sewell, Chia, 1994). If pentacula are borne not in the ovary but in the body cavity, as in *Synaptula hydriformis* or *Staurothyone inconspicua*, they are evidently capable of absorbing coelomocytes (Materia et al., 1991; Frick et al., 1992).

In which state do the gametes undergo resorption ? No special investigations have been carried out to answer this question. However, the often noticed processes of autolysis of gametes, pathological morphology of gametes under conditions of an insignificant number of resorbed cells, suggest the possibility of the initial stages (and sometimes even the entire process) of degeneration of gametes proceeding without the participation or resorbing cells, i.e., so-called intrinsic forces (Caullery, 1925; Masuda, Dan, 1977; Pain et al., 1982; Tyler et al., 1982; Tyler, Pain, 1982b; Ferrand, 1983; Harvey, Gage, 1984). Such "forces" do exist in gametes. Multivesicular bodies, cortical granules, and partly vitelline granules can be regarded as the lysosome system of oocytes (Aizenshtadt, 1984), These structures, like the acrosome of spermatozoa, contain (although not always) a significant assortment of enzymes capable of autolyzing the cell (Ferrand, 1983). Very little in known about the factors triggering autolytic processes in gametes. When visceral ganglia were placed in an organ culture of the gonad of *Mytilus edulis*, intense processes of autolysis and resorption took place in the gonad (Houtteville, Lubet, 1974), i.e., processes of autolysis and resorption are evidently controlled by the neurosecretory system.

Several investigators have described accessory cells of gonads and coelomocytes as resorbing (Gnezdilova, 1971; Masuda, Dan, 1977; Worley et al., 1977; Tyler, Pain, 1982b; Motavkin, Varaksin, 1989) but have not provided a detailed morphological descripion of the processes of resorption nor the resorbed cells as such. Some ambiguity of judging the nature and structure of such cells is due not only to the generally inadequate attention paid to resorption processes, but also differences in the sources of these cells in different animals. Thus, in bivalves, resorption of gametes is effected by hemocytes penetrating the gonad from the adjacent blood vessels as well as by accessory cells already present in it and performing structural-organizational, feeding or control functions. The latter source is represented to a large extent in those bivalves for which the presence of so-called vacuolized cells in gonads is characteristic. Vacuolized cells store

nutrients. Among such mollusks, particular mention may be made of *Mya arenaria* (Coe, Turner, 1938) and *M. japonica* (Dzyuba, Maslennikova, 1987b). The role of accessory or follicular cells in the resorption of gametes in bivalve mollusks is not clearly understood, however. Like many others, Pipe and Moore (1985) presumed their participation in this process but this assumption was not confirmed subsquently (Pipe, 1987b).

As already mentioned, the gonad in sea urchins invariably contains (with rare exceptions, see, for example, Dzyuba, 1978; Harvey, Gage, 1984) accessory cells, one function of which is the resorption of gametes (Ch. W. Walker, 1982). In the testes of sea stars, the resorbing function is performed by axial cells which, before completion of spermatogenesis, formed the structural base for spermatogenic columns (Ch. W. Walker, 1982) or (and) secreted l-methyladenine (Kubota et al., 1977).

How do the resorbing cells engulf gametes? This aspect has been dealt with in some investigations on echinoderms (Beig, Cruz-Landim, 1975; Masuda, Dan, 1977; Ferrand, 1983; Yamashita, Iwata, 1983; Varaksina, 1985). The absorption of groups of spermatozoa or spermatids and different sections of oocytes or ova proceeds by formation of pseudopodia by the resorbing cell. Pseudopodia surround the material resorbed and phagosomes are formed. Another course is the invagination of the plasma membrane of the resorbing cells at the resorption site. Later, the vesicle with the material resorbed contracts within the cell and phagosomes are formed. Sperm groups or separate parts of oocytes (or ova) are at first easily distinguished in phagosomes (Aizenshtadt, Vasetskii, 1986). Phagosomes transform into phagolysomes with heterogeneous content in which concentric membranous structures and unstainable brown colored granules are seen in the final stages of digestion. Such phagosomes become residual bodies removed later perhaps from the gonad cells.

In the resorbing cells, disintegration products of the resorbed material are evidently converted into a soluble form and may pass out of these cells into the coelomic fluid or into the blood stream (Tyler, Pain, 1982a) and be utilized in meeting requirements of the organism, or deposited in the storage cells of pyloric ceca of sea stars, gonad walls of sea cucumbers, mantle of bivalves, etc. In sea urchins, these nutrients may also pass from the gonad (Holland, Holland, 1969) but a bypass of nutrient stream has been detected within the gonad—from accessory cells into the gonad cavity and from there into developing gametes (Takashima et al., 1978). Such a bypass is possible in sea stars also—nutrients emerge from the phagocytizing cells into the space adjoining growing oocytes and the plasma membrane of oocytes forms numerous microvilli (Ferrand, 1983). According to Aizenshtadt and Vasetskii (1986), accessory cells in the ovary of sea star *Patiria pectinifera* absorb the material of phagocytized oocytes and the protein received from the hemal system and provide low molecular precursors of macromolecular synthesis to the growing oocytes. The

intraovarian utilization of dissociation products of unshed oocytes has been suggested in particular for deepwater sea cucumbers and sea stars with lecithotrophic larvae (Pain et al., 1982a, b; Tyler et al., 1985).

Our data may serve to illustrate the prevalence and intensity of resorption processes. Along with glycogen particles, diverse globular structures including phagosomes with resorbed spermatozoa are abundant in the cytoplasm of accessory cells of testes of sea urchins *Strongylocentrotus intermedius* collected long before spawning (in March). A single phagosome may contain 1 to 5-7 absorbed spermatozoa. Layered structures appear in the phagosomes in the late stages of digestion of resorbed material. Postspawning resorption in the testes of sand dollar *Echinarachnius parma* is quite remarkable: accessory cells of gonad are "stuffed" with phagosomes containing resorbed sperm cells. Numerous phagosomes at different stages of dissociation of resorbed material are seen after spawning in accessory cells of testes of sea cucumber *Eupentacta fraudatrix*. The structure of absorbed spermatozoa or spermatids is distinctly discernible in some phagosomes. Residual bodies with concentric membranes constitute the rest of the phagosomes (Kasyanov, 1985a).

Leaving aside further discussion, it must be pointed out here that resorption processes may predominate in the course of the gonadal cycle in bivalves and echinoderms of Peter the Great Bay in the Sea of Japan immediately after spawning as well as in winter and partly in spring. These features have been reported time and again by other investigators too (Gnezdilova, 1971; Dzyuba, 1972; Motavkin, Varaksin, 1989). Mature as well as growing gametes are resorbed.

In animals with maximum fecundity (tens of millions of eggs), resorption processes are concentrated in the postspawning period—they cleanse the gonad of unshed gametes and prepare it for a new gamete generation. Resorption in the redistribution of nutrients from one group of gametes in favor of another has not been observed in these animals. Examples are bivalve mollusk *Crassostrea gigas* and *Mizuhopecten yessoensis*. Resorption processes proceed parallel to gametogenesis in animals with least fecundity (while producing planktotropic larvae). Most growing gametes are destroyed in gonads and redistribution of nutrients probably proceeds in favor of the gamete population (or part of it) awaiting release. Examples are bivalve mollusks *Modiolus difficilis* and sea star *Patiria pectinifera*. In animals with lecithotrophic larvae whose fecundity is insignficant—say a thousand eggs—there may be a special tissue in the gonad, as suggested earlier, which participates in the resorption of excess gametes, for example in sea star *Henricia hayashi*.

The role of the nervous system in controlling reproduction in bivalve mollusks including gametogenic and resorption processes has been detailed in the works of Motavkin and Varaksin (1989) and Zwaan and Mathieu (1992). Nervous and environmental control of reproduction of echinoderms has been detailed in a book by Khotimchenko et al. (1993).

In some species of mollusks and echinoderms, after spawning not only gametes but all acini and gonadal tubes undergo resorption. In some sea cucumbers, total resorption of postspawning gonadal tubules had been recorded (Hyman, 1955; Smiley, Cloney, 1985).

Gonadal cycles

Differences in the course of gonadal cycles in different species with planktotrophic strategy inhabiting the same region may be associated with the intensity of gonial divisions and manifestation of resorption processes and varying duration of different periods comprising the gonadal cycle. Within the same species, the diversity of splitting of the gonadal cycle by different investigators into different stages depending on habitat conditions, reveals the real differences in the course of gonadal cycles in different populations. Such tactical differences are particularly characteristic of species with fugitive r-strategy, as for example *Mytilus edulis*. A comparison of the gonadal cycles of the same species of sea urchins and sea stars inhabiting the northern part of the Sea of Japan and the coast of Japan revealed diversity in these cycles within these seeframe species; the intensity of resorption processes in the gonad is very significant as it influences the overall picture of the gonadal cycle (Kasyanov et al., 1980).

Bivalve mollusks. According to the type of gonadal cycle, Bayne (1976b) distinguished conservative and opportunistic species of bivalve mollusks. Independent of the conditions in a given year, conservative species accumulate nutrient reserves in summer and autumn for gametogenesis proceeding invariably and exclusively in winter and concluding with spawning in spring. Among opportunistic species, gametogenesis is not strictly confined to a definite season and may resume at any time under favorable conditions of food availability, as occurs in *Cerastoderma edule* (Navarro et al., 1989). Under conditions of food inadequacy, mussel *Mytilus edulis* behaves like a conservative species but under favorable conditions, especially under breeding conditons, like an opportunistic one (Rodhouse et al., 1984).

Echinoderms. Annual gonadal cycle in testes is typical of sea stars; the duration of oogenesis, especially in stars with lecithotrophic development, may extend for 2 years (MrClary, Mladenov, 1989; Byrne, 1992).

Species of sea urchins with planktotrophic larvae can be regarded as opportunistic. The structural features of the gonads of sea urchins with large accessory multifunctional cells make for high lability of gametogenic processes in the gonad and thus it is possible to reorganize the gonadal cycle depending on prevailing conditions (Byrne, 1990; Pearse, Cameron, 1991; Yakovlev, 1979; 1993).

Gametes and Fertilization

The relationship between egg size and type of development established about a century ago continues to be analyzed even today from various evolutionary and ecological viewpoints as well as in different groups of marine invertebrates including mollusks and echinoderms (Emlet et al., 1987; McEdward, Carson, 1987; McEdward, Coulter, 1987; Sinervo, McEdward, 1988; Lessios, 1990). On the example of echinoderms inhabiting both sides of the Panama isthmus, Lessios showed that egg dimensions of echinoderms on Pacific and Altantic sides of the isthmus varied variously over the past three million years from the time of formation of this isthmus. On the Pacific coast with a high primary production, egg size of echinoderms with planktotrophic larvae became smaller during this period compared to related species with planktotrophic larvae inhabiting the Altantic coast with a small primary production. Thus, it can be said that egg size has been subjected to factors of selection—large egg size is needed for less primary production and hence larvae feeding on phytoplankton (Emlet et al., 1987; Sinervo, McEdward, 1988).

Gamete dimensions serve as an important characteristic of the reproductive strategy of a species and, being the result of gonadal activity of the parent organism, largely determine the developmental pattern. The relationship between egg size and type of development among echinoderms was established more than ninety years ago; this correlation in the last decades has been well interpreted (McEdward, 1987) in terms of reproductive strategy. As a rule, echinoderm eggs up to 200 μm diam are characterized by development with planktotrophic larvae; a comparatively small number of species have eggs 300-600 μm diam, usually producing lecithotrophic larvae. Eggs of large diameter (over 700 μm) are produced by species with lecithotrophic larvae or direct development; eggs of brooding species attain maximum diameter (McClintock, Pearse, 1986).

Eggs of bivalve mollusks are generally smaller than eggs of echinoderms but, within their size range, the same relation repeats: planktotrophic larvae develop from eggs of small diameter, 40-85 μm, and lecithotrophic larvae with a short pelagic phase from eggs of 90-140 μm while eggs 150-200 μm diam generally develop without a larval stage (Ockelmann, 1965b). The correlation between egg size and the type of development becomes evident on analyzing literary data. In some groups, for example in nudibranch mollusks, the above relationship does not hold due to the use of egg envelopes or other formations outside the egg as nutrient reserve (Clark, Jensen, 1981).

Let us examine in greater detail the shape and structure of gametes of bivalves and echinoderms.

Bivalves. The sperm structure in bivalves is probably dependent on the

structure of their egg envelopes and insemination characteristics (Ockelmann, 1964; Popham, 1979; Franzen, 1983; Bernard et al., 1988). We studied the relationship between size and shape of spermatozoa and egg dimensions as well as the type of development in different families of bivalves (Drozdov, Kasyanov, 1985b). The size and form of the spermatozoon nucleus and its DNA content vary widely even within the same family of mytilids (Tuturova, 1989). It is possible that the latter differences were caused by polyploidy of some species.

To date, optical microscopic studies have been done of the morphology of the spermatozoa of more than 100 species of bivalve mollusks and electron microscopic studies of more than 40.

In general, external insemination and a typical flagellate sperm cell is characteristic of bivalves. However, within this general structural plan, the morphology of spermatozoa of bivalves varies greatly.

Go for the internal structure of spermatozoa of different families of bivalves, the structural diversity of the acrosome may be noted. It consists of an acrosomal vesicle and periacrosomal material wholly or partly surrounding it. A basal ring is seen in the distal part of the acrosomal vesicle of many spermatozoa and the material of the ring reacts in the course of activation with microvilli of the egg (Hylander, Summers, 1977; Healy, 1989, 1995; Keys, Healy, 1999). The periacrosomal material may be represented as an axial rod. The axial rod is lacking is some species, for example in freshwater mollusk *Ligumia subrostrata* (Trimble, Gaudin, 1975); it is very long in others, for example in the spermatozoa of brooding mollusk *Transenella tantilla* (family Veneridae). In the latter, for a head length 17 μm, the acrosomal axial rod is about 15 μm long (Thompson, 1973). The family Mytilidae is notable for its long axial rod (Drozdov, Reunov, 1986b; Hodgson, Bernard, 1986a, b). Spermatozoa of teredinid *Zachsia zenkewitchi*, unique from the viewpoint of reproduction as a genus with dwarf males, are prominent among spermatozoa of other teredinids in the smallest size acrosome and absence in it of an axial rod of actin filaments. Before spawning, sperm balls about 100 μm diam are formed in the testes, with spermatozoa heads turned to the periphery of the ball (Drozdov et al., 1997). In cardiids and tridacnids, the proximal part of the nucleus more or less penetrates the acrosome of spermatozoa like a projection (Sousa, Asevedo, 1988; Sousa et al., 1995; Keys, Healy, 1999).

In some species, the acrosome is located not in the apical part of the head, but adjoins its midpart, for example in *Myodora brevis* from Anomalodesmata (Popham, 1979). In the course of spermiogenesis, the acrosomal granule forms in the anterior part of the spermatid but shifts later. A similar displaced definitive position of the acrosome was detected in the family Lyonsiidae in brooding mollusks *Lyonsia norvegica* and *L. ventricola* (Franzen, 1955; Kubo, Ishikawa, 1978). Kubo (1977) calls such an acrosome found in brackish water species *Laternula limicola* (family

Laternulidae) a temporary acrosome since it occupies the apical part of the spermatid only during spermiogenesis, shifting later to the rear of the mitochondrial section of the spermatozoon. The function of the temporary acrosome is not clear. Possibly, having lost the original function of establishing contact of spermatozoon with ovum, the temporary acrosome is used as a nutrient reserve.

The acrosomè is situated above the nucleus and in its anterior invagination. The latter reaches maximum depth in the family Mytilidae in which it is transformed into a nuclear axial canal. In spermatozoa of subfamily Mytilinae, the axial rod pierces almost right through the nucleus along the apical-basal axis (Drozdov, Reunov, 1997; Kafanov, Drozdov, 1998). Significant intraspecific variations of length of axial rod of spermatozoa have been observed in *Musculus discors* (Kafanov, Drozdov, 1998). The posterior invagination of the nucleus is poorly visible. In the midpart of spermatozoa spherical mitochondria are seen, whose number may vary from 4 to 14 in different species. Mitochondria are surrounded by two mutually perpendicular centrioles. A pericentriolar radial complex is present. In spermatozoa of *Scorbicularia plana*, mitochondria extend forward along the nucleus (Sousa et al., 1989).

The proximal centriole of spermatozoa in bivalve mollusk *Tridacna maxima* is connected to a small depression at the base of the nucleus with a fine layer of pericentriolar material (Keys, Healy, 1999). The pericentriolar radical complex of spermatozoa in oysters fixes the distal centriole to the plasma membrane with nine bifurcated radial fibrils. Glycogen particles are found here itself in the midpart of spermatozoa (Bozzo et al., 1993).

Atypical apyrene sperm cells found in addition to the common form in *Montacuta tenella* of family Montacutidae (Ockelmann, 1965a) and in *Mysella bidendata* of family Galeommatidae (Ockelmann, Muus, 1978) can be regarded as a rarity. They probably participate in the formation of spermatophores. In *Mysella tumida* (hermaphrodite species), spermatophores enter the branchial cavity of a female and the transferred spermatozoa attaches to the branchial filaments by microvilli originating from the acrosome. Spermatozoa may be active in this state for a few months until the moment of insemination, which occurs in the branchial cavity (O' Foighill, 1985).

Eggs of bivalves range 40-360 μm in diam. Like the eggs of other Bilateria with external insemination (Mazzini et al., 1984), they are surrounded by vitelline and gelatinous membranes or envelopes. The thickness of the vitelline membrane is about 1-2 μm while that of the gelatinous envelope may exceed 10 μm. Data on the gelatinous envelope of eggs in bivalve mollusks are very scant. These envelopes are usually transparent, have a soft consistency, and do not preserve well after fixation. In many mollusks, for example *Spisula solidissima* and *Chama macerophylla*, the gelatinous envelope poses no barrier to the spermatozoon and it

freely swims through (Hylander, Summers, 1977); on the other hand, dense egg envelopes, for example in species of family Astartidae (Kaufman, 1977), obstruct sperm movement. In species of genera *Musculus* and *Musculista*, eggs may be held in filament-like clutches. Gelatinous clutches are common is amphibians and are found in gastropod mollusks and polychaetes among marine invertebrates; these are rare in bivalve mollusks. The mortality of germ cells in the clutch ten times lower compared to free-floating ones. However, limitations of developing in clutches are also high as they affect the processes of insemination and hatching of eggs and metabolism between embryos and external environment (Strathmann, Stathmann, 1989).

According to Hylander and Summers (1977), during activation of sperm in the course of fertilization the axial rod of the acrosome surrounded by the membrane of the acrosomal vesicle changes into an acrosomal process which establishes contact with the plasma membrane of the microvilli of the ovum. Significantly, the axial rod does not elongate during activation and the acrosomal process is as long as before. The considerable elongation of the axial rod during artificial activation of the spermatozoa (Dan, Wada, 1955) is perhaps an artifact (Hylander, Summers, 1977). Thus, the length of the rod indicates the thickness of the barrier to the ovum (in the form of vitelline or gelatinous envelope) through which the sperm cell cannot actively pass because of obstruction and sends out the acrosomal process in front. For example, the process length of about 1 μm in *Spisula solidissima* and *Chama macerophylla* is in conformity with the thickness of the vitelline membrane; the process length of 3.5-8 μm in Mytilidae probably represents the total thickness of vitelline and dense layers of the gelatinous envelope. The elongated form of the sperm head in some families of bivalves has probably evolved as a result of development of a protective membrane on ova. The elongated, conical form of the head as well as the presence of a long axial rod facilitate overcoming these barriers during fertilization.

As a rule, egg envelopes are distinctly manifest in bivalve mollusks with large size eggs and a positive relationship between egg size and length of sperm head evidently reflects the dependence of size (and shape) of sperm cell on development of egg envelopes.

Development with lecithotrophic larva or direct development is characteristic of mollusks with eggs of large diameter which usually have well-developed envelopes. A comparison of length of sperm head with type of development revealed that long head length is characteristic of mollusks with lecithotrophic larvae or direct development (on average, in species with planktotrophic larva, sperm head length is 3.6 μm, and in species with lecithotrophic larvae or direct development, 7.0 μm.) However, the relationship of thickness and density of egg envelopes with egg size and the type of development cannot be regarded as absolute:

egg envelopes may be well developed even in species with small eggs and planktotrophic larvae (*Mytilus edulis* and *Crenomytilus grayanus*). The coefficient of correlation between egg diameter and sperm head is 0.66 (r_{05} = 0.37) considering species with lecithotrophic and planktotrophic larvae as a single group. Within each group, made up of species with indentical type of development, the correlation coefficient is considerably low (for species with lecithotrophic larva, r = 0.36 at r_{05} = 0.63; for species with plankto-trophic larva, r = 0.42 at r_{05} = 0.49); the converted correlation coefficient z calculated by combining both groups with n^{-4} degrees of freedom for each group is equal to 0.398 at r_{05} = 0.404. Thus, along with obvious differences in sperm head length between groups of species with different types of development, there is a tendency within each group for the sperm head length to increase as egg diameter increases.

Sea cucumbers. After analyzing the sperm structure in echinoderms, many investigators have concluded a dependence between sperm structure and insemination conditions (Colwin, Colwin, 1957; Atwood, 1975; Chia et al., 1975). New data from optical and electron microscopy on the structure of gametes and their membranes as well as our material of gamete structure in 12 species of echinoderms permitted us to offer a more complete description of this dependence (Drozdov, Kasyanov, 1985a).

Eggs of sea cucumbers of species *Stichopus japonicus* and *Eupentacta fraudatrix* investigated by us do not differ in size from those of other sea cucumbers which have the largest size range among eggs of echinoderms. Egg diameter in *Synaptula vittata* is 50 μm and in *Enyphiastes eximia* about 3,500 μm. Sea cucumbers with egg diameter less than 100-200 μm generally have planktotrophic larvae but with egg diameter exceeding 600 μm develop without larvae (Tyler et al., 1985).

Eggs of all sea cucumbers as well as the species studied by us are surrounded by vitelline and gelatinous envelopes. The width of the gelatinous envelope in *Cucumaria echinata* is 50-70 μm (Ohshima, 1921) and in *C. elongata*, 40-60 μm (Chia et al., 1975). A micropylar appendage on the animal pole has been noticed in the form of an oocyte outgrowth in contact with follicular cells. The structure of the gelatinous envelopes of eggs of *E. fraudatrix* is similar to that in other sea cucumbers. According to the data of Lönning (1976), the radial striation on the gelatinous envelope is formed by microvilli of the egg. At the moment of maturation, which occurs in water immediately before fertilization, the striated layer stretches and swells and the dense outer layer become indistinguishable.

Size, shape, and ultrastructure of sperm cells in an overwhelming majority of sea cucumbers are similar to the corresponding features of the sperm cell in *E. fraudatrix* (Drozdov, Kasyanov, 1985a). A nucleus of the same shape is seen in the spherical or ellipsoidal head and a large acrosome is present in the anterior fossa of the nucleus. The acrosome consists of a

spherical acrosomal vesicle and periacrosomal material surrounding it. The midpart is indistinctly set off from the head and, as in all echinoderms, consists of a single annular mitochondrion surrounding two centrioles. The fat globule is also seen here. The pericentriolar radial complex is distinctly seen in the sperm cell of sea cucumbers. This complex joins the distal centriole with the plasma membrane. Sperms of this description are seen in *C. miniata* (Fontaine, Lambert, 1976), *C. lumbrica* (Atwood, 1973b), *Leptosynapta clarki* (Atwood, Chia, 1974), *Thyone briareus* (Summers et al., 1971), and *Holothuria tubulosa* (Plandellorens, Subirana, 1975).

The gelatinous envelope of the egg as described above poses a barrier to the spermatozoon as a result of which it cannot penetrate the envelope. Penetration of the spermatozoon through the gelatinous and vitelline membrane proceeds without active participation of the sperm flagellum, by the contracting ability of the cortical layer of the egg which pulls the sperm inward and draws it through the egg membranes. Contact of the sperm cell with the ovum preceding these processes is made by the acrosomal process which is formed of periacrosomal material during the sperm cell approach to the gelatinous envelope. The acrosomal process attains long length, somewhat exceeding the thickness of the gelatinous envelope. The length of the acrosomal process in the sperm cell of *Thyone briareus* can reach 90 μm (Summer et al., 1971).

Cucumaria pseudocurata have spermatozoa which differ somewhat from the typical sperm cells. The sperm head is in the form of a pellet 5.5 × 1.2 × 0.8 μm (Atwood, 1975). Atwood assumed that the acrosome in the spermatozoa of this species is displaced surficially to the center of the nucleus. It is quite possible however, that it remains in the initial position but the nature of sperm swimming (acrosome downward) differs from the norm, as a result of which the acrosome (and centrioles according to Atwood) gives the impression of moving on the opposite lateral surfaces of the head. Atwood associates the pelletlike shape of the head with the need for the sperm cell to penetrate the dense gelatinous envelope and possible formation of spermatophore.

Brittle stars. Eggs 100-200 μm diam are common in brittle stars with planktotrophic development while the range is 400 to 900 μm in ovoviviparous species (Hendler, 1975, 1988, 1991; Byrne, 1991). However, in viviparous *Amphipholis squamata*, the egg diameter is only 100 μm and nutrient supplements from the mother organism enter the embryo through specialized sinuses in the wall of the pouch in which embryos develop (Walker, Lesser, 1989).

Sea stars. The diameter of eggs of sea stars investigated by us—*Distolasterias nipon, Aphelasterias japonica, Asterias amurensis, Patiria pectinifera,* and *Henricia hayashi*—falls in the ranges known for this class, i.e., 100-3,540 μm. The upper limit corresponds to the diameter of eggs of

Antarctic sea star *Notasterias armata*, which broods the embryos until the juvenile stage (McClintock, Pearse, 1986). The thickness of the gelatinous envelope of sea star eggs is 5-20 μm. Some species reveal a radial structure of the envelope formed by microvilli of the egg (Lönning, 1976; Monroy, Rosati, 1983). As in some other groups of animals, viviparity and feeding from the mother organism or siblings does not need a large amount of egg yolk; hence in groups more advanced in this respect, reduction in egg size is observed. Sea stars *Patiriella vivipara* and *P. parvivipara* represent distinct examples of such animals. These are tiny sea stars with simultaneous hermaphroditism, intragonadal insemination and intragonadal brooding, with offspring emerging in the stage of highly simplified brachiolaria (Byrne, 1995).

Dimensions and ultrastructure of the sperm cells of *A. amurensis* described by us are similar to those of other sea stars. The head may be spherical or slightly flattened. The acrosome, consisting of the acrosomal vesicle and periacrosomal material, is situated in a large dish-shaped anterior fossa of the nucleus. The acrosomal material with a complex contour surrounds the vesicle on all sides. Dense-electron structures, probably representing actin polymerization centers during formation of the acrosomal process are seen in the basal region of the acrosomal vesicle. The pericentriolar radial complex is developed. This is the ultrastructure of spermatozoa in *Asterias forbesi* (Bernstein and Fahrenbaker, 1960), *Marthasterias glacialis* (Sousa, Azevedon, 1983), and *Ctenodiscus crispatus* (Summers et al., 1971).

As in the case of sea cucumbers, the sperm cell is activated on coming into contact with the gelatinous envelope and an acrosomal process 18-28 μm long is formed (Dan, 1954; Colwin, Colwin, 1957; Dale et al., 1981). The substance inducing the acrosomal reaction has been isolated from the gelatinous envelope of *Asterias amurensis* (Uno, Hoshi, 1978). In the course of acrosomal reaction, the process reaches the egg plasma membrane and later the sperm cell is pulled through the egg envelopes to enter the egg.

Sea urchins. The diameter of eggs of sea urchin species studied by us—*Strongylocentrotus nudus*, *S. intermedius*, *Echinarachnius parma*, *Scaphechinus mirabilis*, and *Echinocardium cordatum*—is typical of sea urchins. It varies within the class from 54 to 1,470 μm. Planktotrophic plutei develop from eggs up to 345 μm diam; egg diam was 280 μm in one species of cidaroid urchin with facultative planktotrophic plutei; two species with egg diam 300-350 μm pass the stage of lecithotrophic plutei; finally, a definitive specimen develops bypassing the larval stage from eggs exceeding 400 μm diam (Raff, 1987). Yolk-rich floating eggs of bathyal sea urchin *Araesoma fenestratum* (Cameron et al., 1987) and Antarctic sea urchin *Abatus nimrodi* which brood the young (McClintock, Pearse, 1986) are the largest in size.

A study of fertilization kinetics of eggs of sand dollars showed that the

gelatinous envelope of their eggs while considerably enlarging the egg size as a whole, performs the role of seizing spermatozoa and enhances the chances of egg fertilization (Podolsky, Iribarne, 1995).

The gelatinous envelope of the egg consists of sulphomucopolysaccharides secreted by the egg itself in the late stages of oogenesis (Monroy et al., 1984). The material of the gelatinous envelope is scattered by the material contained in the spermatozoon (Yamada, Aketa, 1983). As in *S. intermedius*, the gelatinous envelope of eggs of other sea urchins has a micropyle (Lindahl, 1932; Piatigorsky, 1975). The fibrillar gelatinous envelope described for eggs of *Echinarachnius parma* and *Scaphechinus mirabilis* is also present in *E. brevis* and *Dendraster excentricus* (Onoda, 1938; Chia, Atwood, 1982).

The ultrastructure of the gelatinous envelope consists of filaments 2-5 nm wide submerged in an amorphous material (Kidd, 1978). In some species, for example in *Lytechinus pictus*, the gelatinous envelope is formed of several concentric layers about 1 μm wide. Microvilli of the egg reach the internal layer adjoining the vitelline membrane. Neither acidification of the sea water nor passing eggs through a capron net, common methods of removing the gelatinous envelope, removes the filaments of the internal layer of the gelatinous envelope (Kidd, 1978). This aspect should be taken into consideration when analyzing factors causing the acrosomal reaction of the sperm cell. Although the main bulk of molecules inducing the acrosomal reaction of the sperm cell is fixed in the vitelline membrane of the egg, some are contained in the gelatinous envelope (Monroy et al., 1984).

Spermatozoa of sea urchins differ from those of other echinoderms in the conical shape of the sperm head. Its length varies from 1.3 to 8.4 μm (Kaufman, 1977; Amy, 1983; Raff et al., 1990). Our description of the internal structure of the sperm cell is based on the example of the sperm cell of *S. intermedius* (Drozdov, Kasyanov, 1985a). This description may be supplemented with a brief description of the ultrastructure of spermatozoa of two other species. In the spermatozoa of *Echinarachnius parma*, according to the data of Summers and Hylander (1974), a relatively small apical acrosome consists of an acrosomal vesicle 0.3 μm diam and periacrosomal material that fills the anterior fossa of the extended nucleus. In the midpart, generally a single annular mitochondrion, two parallel centrioles, and stray lipid globules are found. The spermatozoa of *Echinocardium cordatum*, according to Afzelius and Jessen (Afzelius, 1955; Jessen et al., 1973), stands distinctly apart among spermatozoa of other species of sea urchins in shape of the acrosome, consisting of a long (2.5 μm) postacrosomal rod that extends from the deep invagination of the nucleus to the acrosomal vesicle separated by this rod at a distance of about 1 μm from the apical surface of the nucleus.

The pericentriolar radial complex characteristic of the spermatozoa of other echinoderms is lacking in the spermatozoa of all sea urchins.

In echinothurid sea urchins, the spermatozoa have a long head (4-7 μm) with slender, long nucleus, and a small acrosome. In the course of acrosomal reaction, a short acrosomal process about 0.5 μm long and 0.1 μm broad forms in the sperm cell (Amemiya et al., 1980). The short acrosomal process (often shorter than 1 μm) is formed during activation of the sperm cell and is characteristic of the sperm cells of sea urchins. A comparatively long acrosomal process exceeding 4 μm forms only in the sperm cell of *E. cordatum*. Sea urchins do not need a long acrosomal process since, on contact with the egg, the sperm cell actively swims through the gelatinous envelope without an acrosomal reaction. If the gelatinous envelope removed from an egg is placed in a suspension of sperm cells, the latter move in it at random and gather in the space occupied priorly by the egg itself. The acrosomal reaction is noticed only in sperm cells coming into contact with the vitelline membrane (Summers, Hylander, 1974; Aketa, Ohta, 1977).

Echinoderms. General. The size range of eggs of echinoderms is 50-3,500 μm. A few species of sea cucumbers reach the limits of this range: *Synaptula vittata* 50 μm and *Enyphiastes eximia*, 3,500 μm. The diameter of eggs of echinoderms of other classes falls essentially in the range 100 to 1,000-1,300 μm. Within these limits, two groups of species are distinguished: with egg diameter 100-200 μm and 800-1,300 μm. The first group is characterized by high fecundity (millions to tens of millions of eggs) and the presence of planktotrophic larvae in the life cycle, and the second group by low fecundity (100 to 1,000 eggs) and the presence of lecithotrophic larvae or direct development.

Echinoderm eggs are surrounded by vitelline and gelatinous membranes. We were not able to establish a clear relationship between egg and envelope size, although envelopes of large eggs rich in yolk are more often very complex in structure.

Enchinoderm spermatozoa have a fairly simple structure characteristic of a typical sperm cell. Sperm heads measure 1-9 μm. Two groups of spermatozoa can be distinguished according to the form of the head: spermatozoa of sea urchins and those of other echinoderms. Spermatozoa of sea urchins have a conical head, small acrosome, parallel disposition of centrioles, and lack a developed centriolar radial complex. Spermatozoa of other classes of echinoderms have a spherical or ellipsoidal (with long axis, usually perpendicular to the sperm axis) head and comparatively large acrosome; parallel, oblique or mutually perpendicular disposition of centrioles; and developed pericentriolar radial complex. These two groups are further distinguished by length of acrosomal process. Its formation in sea urchins and other echinoderms during fertilization is induced by different layers of egg coats. Acrosomal reaction in

spermatozoa of sea urchins is caused by the interaction of the sperm cell with receptors of the vitelline membrane of the egg (Monroy et al., 1984) and an acrosomal process 0.5-4 μm long is formed; it is adequate to perforate the vitelline membrane. Spermatozoa of sea cucumbers, sea stars, and brittle stars are activated by contact with the outer layer of the gelatinous envelope and a long acrosomal process is formed (length 5-90 μm) which later penetrates both the gelatinous and vitelline membranes. We could not find data on the acrosomal reaction of the spermatozoa of sea lilies but the shape and structure of their sperm cells suggest formation of a long acrosomal process in them.

Neither our data (Drozdov, Kasyanov, 1985a) nor that available in the literature revealed a clear dependence between size of female and male gametes. However, the size and structure of male gametes depend on thickness and consistency of egg coats. This relationship differs in sea urchins and other echinoderms. The original type, the principal one for echinoderms, has a spherical or near-spherical sperm head.

Data have recently become available on spermatozoa of echinoderms under special insemination conditions. Spermatozoa of certain species of sea lilies, sea cucumbers, and sea stars lose their original spherical or near-spherical head shape and acquire an elongated or some other shape. Such is the case with spermatozoa of sea lily *Isometra vivipara* (Holland, 1976), sea cucumber *Cucumaria lubrica, C. pseudocurata* (Atwood, 1975; Atwood, Fu, 1974) as well as sea stars of genus *Xyloplax* (Rowe, 1987; Healy et al., 1988), formerly regarded as a distinct class of echinoderms on the basis of various characteristics including sperm structure. However, it has correctly been pointed out that the significant deviations in structure of spermatozoa of *Xyloplax* from the original form of spermatozoa of sea stars may suggest not so much phylogenic deviations of these echinoderms, as differences in type of insemination in common shallow-water sea stars and *Xyloplax* inhabiting waters of deeply submerged timber (Belyaev, 1990). Aberrant spermatozoa have also been detected in deepwater sea urchins with internal insemination; further, *Phrissocystis multispina* exhibits dimorphism of spermatozoa: along with common spermatozoa bearing a single flagellum, biflagellate ones are also present (Eckelbarger et al., 1989). Au et al. (1998) described dimorphism of normal spermatozoa of sea urchin *Anthocidaris crassispina*: the flagella of most spermatozoa are turned backward but in some, forward.

During sperm activation at sea stars, sea cucumbers and brittle stars, the acrosome of considerable dimensions forms a long acrosomal process leading the sperm cell into contact with the egg followed by pulling the immobilized sperm cell through the membrane. In the second type, active passage of the sperm cell through the gelatinous envelope and formation of a short acrosomal process in the immediate proximity of the egg surface take place, i.e., sea urchins "work out" a more streamlined conical and

sometimes elongated-conical head shape. In this class, the length of sperm head probably depends on egg size and degree of development of coats. The elongated head shape of spermatozoa, up to 20 μm, in *Phyllacanthus parvispinus* is characteristic of spermatozoa of sea urchins with direct development and correlates with egg size. Head shape is determined by elongation of the nucleus of spermatozoa and not by shape of the acrosome (Raff et al., 1990).

Thus, echinoderms play different variations of "sperm-egg interaction" (Monroy, Rosati, 1983).

Morphological events in this interaction have been studied in sea urchins and briefly recounted here. The activated sperm cell attached to the egg with its acrosome continues to beat with its flagellum; this beating ceases abruptly later. The contact with the acrosome of the sperm cell activates the egg—a few thousand cortical granules fuse with the egg plasma membrane, exocytosis of their contents occurs, the fertilization membrane separates from the plasma membrane, the plasma membrane temporarily enlarges in area, and long microvilli appear on the egg surface. The fertilization cone is formed as a gigantic microvillus which soon absorbs the immobile sperm cell and later disappears itself. The entire sperm cell enters the egg and, within the egg, the sperm cell again beats with its flagellum. Later, the nucleus and midpart of the sperm cell roll forward and move into the cortical layer. A spermaster is formed around both centrioles of the sperm cell, which initially controls movement of the male and female pronuclei toward each other and later movement of the joined pronuclei to the middle of the egg (Schroeder, 1973; Schatten, 1982). Zygote cleavage commences soon thereafter. Palumbi (1992) and Vacquier (1998) reported on the decisive role of a small number of gene products—receptors disposed on the surface of eggs and spermatozoa (Foltz, Lennarz, 1993; Healy, 1995)—in the reproductive isolation of sessile or poorly mobile marine invertebrates with external insemination. This mechanism of reproductive isolation differs from prezygotic reproductive isolation including, for example, signs of courtship, exhibited by the mobile marine and terrestrial organisms with internal insemination. The sperm receptor of sea urchins reacts with the vitelline membrane of the egg and participates in its activation (Abassi, Foltz, 1994; Guisti et al., 1997). Isolation and sequencing of the bindin gene—egg receptor of sea urchins enveloping the surface of the acrosomal process during the course of fertilization—showed that 95% of bindin amino acids is common for sea urchins separated by 150-200 million years in their genesis; marginal regions of bindin differ greatly in different species and participate in reproductive isolation (Gao et al., 1986; Glabe, Clark, 1991; Foltz et al., 1993).

In bivalves mollusks, cessation of meiosis in oocytes before fertilization is perhaps caused by two proteins, one of which blocks escape from

prophase I and the other blocks escape from metaphase I or interrupts the second meiotic division (Osanai, 1993, 1994). The state of metaphase in unfertilized oocytes is supported by newly synthesized proteins blocking the pathway of dephosphorylation of cycline (Abelmajid et al., 1993; Osanai 1994). The sperm cell penetrates the oocyte in the stage of germinal vesicle or at much later stages of maturation division, bringing the process to completion (Schuetz, 1985; Tamaki, Osanai, 1985; Vasetskii, 1987). The sperm nucleus remains in the cortical layer of the oocytes until completion of meiotic cleavage; later the female pronucleus advances toward the male pronucleus and the joined pronuclei migrate to the zygote center, after which the axis of the first division of cleavage is formed (Kuraishi, Osanai, 1988).

Early development

Bivalves. Eggs of bivalve mollusks undergo complete spiral heteroquadrant cleavage. The unequal dimensions of macro- and micromeres are poorly visible. The furrow of the first cleavage divides the egg into the unequal blastomeres: the smaller AB and larger CD. In the four-celled stage, blastomere D is much larger than the other blastomeres. Among the daughter cells of blastomere D, blastomeres 2d and 4d are distinguishable as they are larger than the corresponding macromeres. Blastomeres 2d and 4d represent the first and second somatoblasts. As a result of cleavage, a ciliated sterro- or coeloblastula is formed; this represents the first larval stage of bivalve mollusks with cilia. A sterroblastula is characteristic of marine bivalves and a coeloblastula of brackish and freshwater mollusks (Malakhov, Medvedeva, 1986). Even at this stage, the derivatives of ectodermal blastomere X (daughter cell of the first somatoblast) form the primordium of the shell gland which represents a clear example of early differentiation of embryonic cells. In the course of gastrulation, daughter cells of the second somatoblast produce enteroblasts (entodermal cells) and mesodermal teloblasts from which transitory mesodermal bands originate later (Ivanova-Kazas, 1977a). An early differentiation of embryonic cells, especially of somatoblasts, is generally characteristic of the entire group Spiralia which includes mollusks. Daughter cells of the first somatoblast initiating development of larval and definitive organs (including the shell) with ectodermal origin are the first in the course of differentiation. Purely larval, provisional organs—pretrochal ectoderm and velum—are differentiated from daughter cells of the first quartet of micromeres 1a-1d. Following them, daughter cells of the second somatoblast are differentiated and comprise the source of mesodermal derivatives of the adult.

The article by Gustafson and Reid (1986) marks an important event in the study of the early development of bivalve. They described the

development of primitive cryptodont protobranch bivalve mollusk *Solemya reidi*. Cleavage of large (270 μm diam) eggs of this species is possibly the only example to date for bivalve mollusks of initial homoquadrant spiral cleavage with equal-size blastomeres.

Incomplete cleavage has not been detected in bivalves.

The gastrula is transformed into a trochophore. In this stage, the shell gland is already everted. The trochophore moves by the beating of cilia of a broad ciliary ring (prototroch) fringing the animal part of the trochophore above the mouth. The mouth leads to the closed blind gut (Ivanova-Kazas, 1977a; Medvedeva, Malakhov, 1983).

According to Ivanov (1937), all the characteristic features of spiral cleavage arose as a result of adjustment development to the trochophore.

The trochophore transforms into a veliger which has a more complex structure compared to the preceding stages. The animal pole of the trochophore grows into a sail or velum in the form of a disk with 3 or 4 ciliated bands (1 or 2 preoral, adoral, and postoral). An apical tuft of sensory cilia is located in the center of the velum. The rest of the larval body is covered with a translucent shell through which the internal organs of the larva are visible.

Sea stars. Egg cleavage in almost all species of sea stars is radial, complete, and quite uniform. The coeloblastula forms as a result of division. Absence of complete cleavage is a distinguishing developmental feature of *Fromia ghardaquana* (Mortensen, 1937). In this sea star, cytotomy of the large egg is preceded by repeated division of nuclei, which then migrate from the center to the periphery of the egg. Separation of cell boundaries in the embryo of *F. ghardaquana* continues for a long time. Delayed cytotomy, compared to nuclear division, also characterizes the large eggs of *Henricia sanguinolenta*. Neither *F. ghardaquana* nor *H. sanguinolenta* has planktotrophic larvae. Yolk lies under the blastoderm in deepwater *Aspidodiadema jacobi* at the blastula stage (Young, Cameron, 1987).

Gastrulation proceeds by invagination. During gastrulation, separation of the mesoderm occurs by separation of the archenteron of coelomic vesicles followed by preferential development of left coeloms. In some species with large eggs, development of mesodermal cells is "rationalized", straightened, and left coeloms separate clearly immediately from the archenteron and develop faster. Examples are *Henricia sanguinolenta*, *Solaster endeca*, and *Crossaster papposus* (Gemmill, 1920).

After gastrulation, the ectoderm of the anterior portion on the ventral side of the gastrula is invaginated. The tip of the archenteron bends in the direction of this invagination and the cells of ecto- and entoderm, with the participation of mesenchymal cells, come into contact and form the oral opening (Abed, Crawford, 1986). The oral opening is situated in the perioral depression and is edged with a ciliated band. The edge of the raised plateau on the ventral side of larva—preoral and anal plates—has

better developed ciliary covers compared to the rest of the larval surface. This stage represents the dipleurula. The marginal ciliary covers later give rise to ciliated bands of the next stage—bipinnaria (Ivanova-Kazas, 1978).

Sea urchins. In the majority of sea urchins, development proceeds with planktotrophic larvae. For egg cleavage in sea urchins, formation of eight animal mesomeres, four vegetative macromeres, and four vegetative micromeres in the 16-cell stage is a characteristic feature. The daughter cells of micromeres are differentiated before other embryo cells and synthesize larval collagen and the extracellular matrix of the blastula cavity even before formation of the larval skeleton of the pluteus (Benson et al., 1990). Immediately before formation of the larval skeleton, maximum expression is noticed of the suBMP gene, one of the genes responsible for spicule formation in the larvae of sea urchins and homologue to gene responsible for the synthesis of morphogenic proteins of human bones (Hwang et al., 1994). Spicule formation is determined by the zygote genome, which is confirmed by the intermediate type inheritance of spicule structure of larvae in interspecific hybrids (Hata, Osanai, 1994). Spicule formation in the larvae of sea urchins is perhaps the result of displacements in the larval stages of processes that were characteristic of the imaginal stage in early evolution (Cameron, 1998). In primitive sea urchins of order Cidaroida, such an early differentiation of larval cells does not occur and micromeres are not formed in the 16-cell stage. In cidaroid sea urchin *Eucidaris thouarsi*, not all pluteus lobes bearing a ciliated band have an internal skeleton. In general, development and metamorphosis of sea urchins of this group are highly peculiar and differ from the commonly accepted description of the development of sea urchins (Emlet, 1988).

On transition to direct development, micromeres are not formed, the fourth division of cleavage is uniform, there is no premature differentiation of larval skeleton, and a definitive skeleton is formed at once (Raff, 1986). The transition from larval to direct development in sea urchins is accompanied by several heterochronisms. As a result, many larval characteristics disappear or are reduced while definitive characteristics are manifest earlier than usual and develop more rapidly (Raff et al., 1989). Heterochronisms cover only part of the radical reorganization of early development on transition to direct development. Rate of cleavage and its type (Parks et al., 1988; Wray, Raff, 1989), blastula structure (Williams, Anderson, 1975), type of determination of embryo cells and their presumptive fate (Wray, Raff, 1989) differ.

Cleavage results in the formation of coeloblastula and gastrulation proceeds by invagination with elements of immigration. In species with a lecithotrophic pluteus or with direct development, a "wrinkled" blastula is formed and its cavity is filled with some amount of yolk; invagination of the archenteron nevertheless continues (Raff, 1987). Formation of the

oral opening in sea urchins, as in larvae of sea stars, transforms the gastrula into a prism, a stage corresponding to the dipleurula in sea stars. Unlike the dipleurula, in this prism, cells of the larval mesenchyma entering the primary cavity of the body form spines of the skeleton of arms, i.e., outgrowths of the larval body. With the development of arms, bearing ciliated bands, the prism is transformed into a pluteus (Ivanova-Kazas, 1978).

Sea cucumbers. A complete, fairly uniform radial cleavage in sea cucumbers leads to formation of a coeloblastula. In some species with yolk-rich eggs, division becomes surficial with formation of blastoderms in the surface layer of the egg. Examples of this type of cleavage are seen in *Cucumaria glacialis* and *Thyonepsolus nutriens* (Mortensen, 1894; Hyman, 1955). Gastrulation proceeds through invagination together with immigration. Development of coeloms in sea cucucmbers is simplified; this simplifiacation is particularly manifest in development of sea cucumbers which do not have planktotrophic larvae.

As in sea stars, the gastrula changes into a dipleurula and later an auricularia, which differs from the bipinnaria of sea stars mainly in the pattern of the ciliated band and degree of development of coeloms (Ivanova-Kazas, 1978).

We now turn to the beginning of the chapter. Is it not true that all events of ontogenesis carry the features of planktotrophic larvae in some animals while the ontogenesis of others carries a firm imprint of its absence? Orientation for larval or direct development sets the course of ontogenesis (Ivanov, 1937).

ECOLOGICAL ASPECTS

Planktotrophic Larvae

Thorson (1936, 1946, 1950), Mileikovsky (1981, 1985) and others have drawn significant inferences from their studies of the ecology of pelagic larvae of marine invertebrates. They evaluated the effect of abiotic and biotic factors on seasonal dynamics and horizontal and vertical distribution of larvae, demonstrated the relationship between different types of larval development and biogeographic affinity of the species, identified the role of larval pool in recruitment of parent populations and formation of new settlements, etc. An acquaintance with the works of Thorson and Mileikovsky is therefore necessary for understanding the basic principles of the ecology of larvae of marine invertebrates. Both this aspect of marine biology and the ecology of reproduction have been intensively studied in the last decade; new facts as well as new correlations are steadily being discovered (Scheltema, 1986; Emlet et al., 1987; Pechenik, 1987, 1999; Young, Chia 1987; Lutz, Kennish, 1992; Seed, Suchanek, 1992; McEdward, 1995; and others). What follows is only a review of some aspects of larval ecology and ecology of reproduction of bivalves and echinoderms.

Energetics of larvae

Populations of species with planktotrophic strategy shed gametes in the period of spawning. They develop after fertilization into planktotrophic larvae and "graze" on phytoplankton in the water body. In turn, they often become prey to predatory zooplankton feeders or benthic filter feeders. Thus, species with planktotrophic reproductive strategy, in the period of reproduction enter into close and diverse trophic relations with pelagic communities and their trophic relationships with benthic communities become complicated. Herein lies one of the most important differences of such species from those with lecithotrophic reproductive strategy (Kasyanov, 1986a).

Energetics of mollusk larvae, which attracted the attention of researchers in the early 1980s, is being actively studied again (Sprung, 1984a, b; Mann, Gallager, 1985; Whyte et al., 1987; MacDonald, 1988; Manahan, 1990;

Pechenik et al., 1990; Rodrigues et al., 1990). On the one hand, this is because of the practical importance of these studies for marine culture and, on the other, the fact that the energetics approach may be used for evaluating interactions of larval plankton and phytoplankton and, more broadly, interactions of bottom and plankton communities.

Bivalves. Embryonic and early stages of larval development of all bivalves are greatly facilitated by yolk which is stored in the period of gametogenesis. In planktotrophic larvae of *Mytilus edulis*, this phase of lecithotrophy or endotrophy extends for the first two days of development at a temperature of +17-20°C and changes into the mixotrophic phase or phase of mixed (yolk and phytoplankton) food. The mixotrophic phase extends at this same temperature up to the eighth day of development, after which the larva takes to pure exotrophy or planktotrophy (Lucas et al., 1986).

Flagellate microalgae serve as the main food of veligers and the peak population of larvae often coincides with the maximum concentration of these microalgae (Kasyanov et al., 1979). At the same time, mollusk larvae readily devour protozoa and bacteria (Baldwin, Newell, 1991). Thus, the stomach contents of bivalve mollusk larvae from St. Lawrence Bay consist of autotrophic Flagellata (below 5 μm) and cyanobacteria (below 2 μm). The predominance of ultraplankton (below 1 μm) in the littoral waters of Shaler Bay, St. Lawrence Bay, and in the stomach contents of larvae suggests that veligers of bivalve mollusks may be an important course for the export of carbon produced by the minute phytoplankton. This function of larvae has been confirmed by other data as well (Baldwin, Newell, 1991; Gallager et al., 1994; Legendre, Rassoulzadegan, 1995). The ingestion of microalgae by oyster larvae depends not only on the size of the edible particles, but also on the growth rate and chemical composition of microalgae (Appelmans, 1994; Baldwin, 1995).

The rate of filtration of food particles (flagellate algae at concentrations of 1.5-5.5 × 10^3 cells/ml water) in larvae of *Mytilus edulis* is 11.4 $\mu l h^{-1}$ $larva^{-1}$ (Riisgard et al., 1980). At a concentration of food particles exceeding 200 μl^{-1}, feeding rate decreases (Bayne, 1976a). At a low concentration of particles, the rate of their filtration and its efficiency increase. Larvae of *M. edulis* cannot efficiently retain particles smaller than 1 μm or larger than 8-9 μm (Riisgard et al., 1980). Dissolved colloidal matter is unsuitable for *M. edulis* larvae as it forms lumps and cements them together. They take well to frozen or lyophilized algae and granulated food comprising macrophytes and detritus, however. Larvae of *Crassostrea virginica* and *Mercenaria mercenaria* do not accept organic detritus or pure bacterial cultures as food (Loosanoff, 1969). According to Khrebtova and Sorokin (1985), larvae of *Ostrea edulis* use microalgae, detritus, bacterial plankton, and dissolved organic matter. Bivalve larvae absorb free amino acids efficiently from water (Manahan, 1983). With a high concentration of free amino acids in water, veligers of oyster *Crassostrea gigas* can completely meet their oxygen requirements; amino acid concentration in the water body is, of course, not high and its increase is possibly only in the demersal layer where larvae spend only part of all their life (Manahan, 1989).

Flagellate algae such as *Monochrysis* and *Isochrysis* which do not have cell walls or do not form toxic substances represent the best larval food (Ukeles, 1969, 1975). Facultative planktotrophy, rare in bivalve larvae, has been detected in lecithotrophic larvae of lucinid clam *Codakia orbicularis*. These larvae can also derive energy through chemosynthetic bacteria localized in their tissues (Alatalo et al., 1984).

The principle of planktotrophic larva as a "device for feeding" is reflected in the characteristics of its energy budget. The larval weight rise can be computed using an empirical dependence of larval weight on shell length. It cultured *Mytilus edulis* larvae, shell length increased by 7-8 μm day^{-1} at a concentration of 50 algal cells μl^{-1} (Jespersen, Olsen, 1982). Jorgensen (1981) recorded a daily shell increment of 6-8 μm for *M. edulis* larvae in the natural population along the coast of Denmark; this corresponds to an increment of 13-16% in weight of entire larval body. A density of microalgae reaching 20-50 cells μl^{-1} has been recorded at times under natural conditions. The daily output of nanoplankton in Danish and Norwegian fjords may reach concentrations of 50 cells of *Isochrysis* or *Monochrysis* μl^{-1} (Jespersen, Olsen, 1982). The incremental rate of shell length does not rise futher at microalgal concentrations exceeding these values.

The high growth rate of *M. edulis* larvae is due to the fact that 43-75% of the entire assimilated food contributes to growth (Jorgensen, 1981; Jespersen, Olsen, 1982); this value is 56-80% in *Ostrea edulis* larvae (Walne, 1965; Gabbot, Holland, 1973). The assimilation efficiency is 31-45% for *M. edulis* larvae and 12.5-40% for *O. edulis* larvae (Walne, 1965; Jespersen, Olsen, 1981). The assimilated food is partly stored as reserve. The storage of these substances is reflected on the curve of relative content of organic matter in larvae: following a significant drop caused by intense development of the larval shell, this parameter doubles before settling and metamorphosis (Lucas et al., 1986). The energy input for metamorphosis can be estimated from the energy content in bivalve larvae (Day, McEdward, 1984). Energy consumption in the metamorphosis of the pediveliger of oyster *Ostrea chilensis* comprises 64.5% of all reserves (Videla et al., 1998). The success of larval metamorphosis correlates with the concentration of lipids and/or proteins contained in the egg (Gallager et al., 1986; Rodrigues et al., 1990). At the same time genetic data suggest a high degree of heritability of larval growth indexes (Hilbish et al., 1993) independent of the level of lipid concentration in the oocyte (Jones et al., 1996).

After analyzing a population of larval plankton and phytoplankton in Ise Fjord (Denmark), Jorgensen (1981) concluded that dense populations of

bivalve larvae cause a significant load on ultraplankton without greatly influencing the primary production generated mainly by phytoplankton organisms of large dimensions.

Analysis of the population dynamics of *Mytilus edulis*, now identified as *M. trossulus*, larvae in Vostok Bay in the Sea of Japan in 1981 summer (Buyanovskii, Kulikova, 1984) led to identification of a station in Tikhaya Zavod', Bay as an entrapped water body in which larvae are trapped. We used the data from this station to derive some approximate energy characteristics of cohorts (groups of same-aged individuals) of *M. trossulus* larvae (Kasyanov, 1987b). The daily coefficient of larval loss was 12%, close to the value reported by Jorgensen (1981). The average rate of daily shell increment during the four days of analysis at 3.2 μm was half the rate of growth observed at high microalgal concentrations. In the waters of Vostok Bay, the density of fine phytoplankton forms was 0.3-0.6 cell μl^{-1}, peaking in summer months at about 1 cell μl^{-1}. Even the latter value is only a tenth of the density required for maximum larval growth (Jespersen, Olsen, 1982). The efficiency of pure growth is somewhat less than the value 0.52-0.63 reported by Jorgensen (1981) and Jespersen and Olsen (1982). The amount of food assimilated by *M. trossulus* larvae in Tikhaya Zavod' Bay is much less than in Ise Fjord (Jorgensen, 1981) as a result of the high (by 2-3 orders) density of *M. trossulus* larvae in the latter region. In terms of organic matter, the consumption of the cohort of *M. trossulus* larvae in Tikhaya Zavod' Bay is 1.5-1.6 mg Cm^{-3}. The biomass of fine phytoflagellates in Vostok Bay in summer months is about 20% of the total biomass of phytoplankton which, in terms of organic matter, works out to 2.9-4.5 mg Cm^{-3} (Konovalova, 1984). Thus, larvae of typical species with planktotrophic strategy, *M. trossulus*, considerably strain the nutritional resources of fine phytofalgellates in Vostok Bay. This conclusion holds if assumptions about the plankton-bearing station mentioned above for trapping larvae are justified and there is no significant "contamination" of the original cohort with larvae of other cohorts. Another assumption concerns the applicability of empirical formulae derived for cultured larvae of edible mussels in Denmark to the natural populations of close species in the Sea of Japan.

Echinoderms. According to Strathmann (1971), echinoderm larvae ingest particles less than 65-86 μm diam and less than 100-200 μm long. The filtration rate of particles from water is 0.5-4.3 $\mu l\ min^{-1}$; filtration on average proceeds at 0.3-0.6 $\mu l\ min^{-1}\ mm^{-1}$ of the ciliated band. Maximum filtration rates of particles from water vary from 1-2 $\mu l\ min^{-1}$ in early bipinnaria to 6-10 $\mu l\ min^{-1}$ in late bipinnaria of sea star *Dermasterias imbricata* (Hart, 1991). The filtration rate drops as algal concentration rises. When the particle concentration is very high (over 5,000-10,000 cells ml^{-1}), the ciliated band can no longer hold the particles. At algal concentrations exceeding 50,000 cells ml^{-1}, developmental deformities and death of larvae are possible; the intestine of such larvae is clogged with food and their feces contain several whole, undigested algae (Strathmann, 1971; Barker, 1978a).

During intensive feeding, larvae cannot efficiently choose one or discard another type of algae. However, the filtration rates of different types of algae differ and one type can influence the filtration rate of another by increasing or decreasing it (Strathmann, 1975a). The nutritional quality of different types of edible particles has not been well studied. Not enough information is available to judge the role of bacteria and dissolved organic matter in the feeding of echinoderm larvae under natural conditions. In a laboratory culture, the intake of amino acids can cover up to 76% of the energy budget of the pluteus of *Strongylocentrotus purpuratus* (Manahan, 1983). The dissolved organic matter may serve as an important source of energy for the pluteus of *Echinocardium cordatum* (Vyshkvartsev, Sorokin, 1978). Free amino acids can form an additional food source for *Dendraster excentricus* larvae (Burgh, Burke, 1983). The efficiency of ciliated bands in retaining particles under 2-3 μm size is poor and much of the larval growth is observed during active feeding on phytoplankton. Larvae of Antarctic sea star *Porania antarctica* and *Odontaster* sp., which grow in water that is very poor in phytoplankton, rely exclusively or predominantly on bacteria and absorb dissolved organic matter (Rivkin et al., 1986; Bosch et al., 1987b) whose concentration is quite constant and high in Antarctic waters. Planktotrophic (exotrophic is a better term) larvae of deepwater echinoderms can similarly be assumed to survive on bacteria and dissolved organic matter (Rivkin et al., 1986; Bosch et al., 1987b).

In their studies on larval growth of sea star *Paracentrotus lividus* in cultures, Fenaux et al. (1985) demonstrated that the growth rate of pluteus doubled on 5-fold rise of food concentration (flagellate alga *Hymenomonas elongata*). Under optimal food conditions, the caloricity of larvae rose from 0.71 to 9.21 cal $specimen^{-1}$. The annual concentration of fine phytoflagellata in Villefranche Bay enables *P. viridus* larvae to remain in plankton for more than a month. The low density of phytoplankton which provides chlorophyl *a* concentration of 0.5-5 $\mu g\ l^{-1}$ does not make for planktotrophic feeding of larvae of echinoderms and other invertebrates. Such concentrations are noticed in Antarctic waters and occasionally in temperate and tropical waters (Rivkin et al., 1986).

A comparison of the larvae of three species of sea stars of genus *Patiriella* with different reproductive strategies with respect to rate of oxygen demand demonstrated that planktotrophic larvae of *P. regularis* have a very high metabolic rate per unit mass compared to planktonic lecithotrophic larvae of *P. calcar* and especially with demersal lecithotrophic larvae of *P. exigua* by 12 and 21 times respectively (Moreno et al., 1995).

Larval cohort

The immense reproductive potential generated by species with planktotrophic strategy is realized in the form of numerous larvae invading the pelagic zone. The larval cohort (i.e., the aggregate of larvae produced by spawning individuals in a population in a given period) has its own spatial structure and temporal dynamics which significantly influence the age structure and spatial organization of benthic populations. The space-time organization of larval cohorts is determined in turn by the space-time organization of parent populations; reproductive pool of gametes produced by the parent organisms; functional characteristics of larva as pelagic organism; and habitat conditions in the pelagic zone.

Short-term advantages of the settlement of species by use of larvae lie in reduced competition between progeny, parents, and members of the same cohort, rapid settlement and colonization of new habitats, and reduced risk of inbreeding. Long-term advantages include minimization of mortality should the local habitat be damaged and ease of resettlement after conditions improve. The weak aspects of this life cycle scheme are the possible drift of larvae from favorable habitats, their high exposure to predators, and additional expense due to delay in metamorphosis in the absence of specific signals for its onset (Pechenik, 1999).

The larval cohort constitutes the youngest members of the benthic population and isolation of this cohort from all other individuals of the population enables study of size, population dynamics, stability of recruitment, age distribution, mortality, and other characteristics independent of the parameters of the main, benthic population (Kasyanov, 1986b). It has become clear in recent years that larvae are distributed in patches in spaces (Pedrotti, Fenaux, 1992; Martin et al., 1997). They concentrate at places where the density of water body is disturbed—pycnoclines, turbulent fronts, etc. (Pineda, 1991). Such aggregates could be a behavioral response to the high concentration of phytoplankton in these zones and depend on local hydrodynamics (Metaxas, Young, 1998c). Thus the chaotic dynamics of larvae in a patchy medium might well promote the evolution and support the settlement of species (Jablonski, Lutz, 1983; Holt, McPeak, 1996).

Horizontal distribution

The disposition of parent populations and types of currents—steady, tidal or other types—constitute a decisive factor in horizontal distribution of larvae. The more complex the general pattern of steady and intermittent currents in a given water body, the more complicated and less predictable the horizontal distribution of larvae. The role of currents running along the coasts and ocean currents in the dispersal of larvae and formation of the distribution range of the species have been examined on p.108. The

relationship between larval transport and hydrodynamic processes has been analyzed in reviews by Young and Chia (1987) and Shanks (1995). Among hydrological factors important for larval transport at the site of settling, mention should be made of water turbulence caused by wind currents. Annual variations of wind currents largely determine the variability of settlement of bivalve mollusks *Cerastoderma edule* and *Mytilus edulis* from year to year (Young et al., 1998).

As early as 1941, Korringa (1941) reported on the predominantly passive distribution of the larvae of *Ostrea edulis*. Larval distribution agrees most satisfactorily with the hydrological features of the water body in entrapped water masses with low flow rates or intense stratification which restricts vertical mixing (Andrews, 1979; Epifanio et al., 1984). Examples are some estuarine regions as well as small marshes and bays. Larval distribution is complicated for analysis in estuaries with a high yield of fresh water, powerful mixing during high tides, and steady horizontal gradient of salinity.

The distribution of larvae of oysters *Crassostrea virginica* and *Ostrea edulis* in various estuaries of northestern USA and western Europe does not conform to any single pattern: it differs in different estuaries, geographic zones, periods of tidal cycle, etc. The actual role of active behaviour of larvae in selecting the vertical level in an estuarine water body with stratified salinity has not been evaluated thus far (Stancyk, Feller, 1986). Analysis of the distribution of echinoderm larvae in Kiel Bay, with characteristics of an estuary, showed that they behaved like passive particles during horizontal as well as vertical movements without manifesting active "animal navigation" (Banse, 1986). Since hydrological factors determine the dispersal of larvae, the reproductive success of parent organisms primarily depends on favorable hydrological factors. Such a combination of factors is usually seen around tropical islands and reefs and within lagoons. The result is that plankton in these regions is rich in larvae (Cameron, 1986a).

Larvae of bivalves and echinoderms are dispersed by currents within the water body mainly above the areas of parent populations and a little away from them. This ensures a long life span of benthic communities (Mileikovsky, 1977). On the Yugoslav coast of the Adriatic Sea there are thus more larvae of mussel *Mytilus galloprovincialis* in the closed water bodies where mussels are cultivated, compared to populations in open areas (Brenko, 1974). In Posjet Bay, *Mizuhopecten yessoensis* larvae are more (up to 300/m^{-3}) at places of ridge banks but few (30-60/m^{-3}) in the open regions (Belogrudov, 1980). Larvae of scallops *Argopecten irradians* remain above their parental colonies (Arnold et al., 1998). A comparison of the settlement sites of scallop *Placopecten magellanicus* on the Atlantic coast of Canada with larval distribution shows that larvae remain in the region of parental colonies and only an insignificant proportion of them are carried

away by currents (Tremblay, Sinclair, 1988). As pointed out before, the characteristics of Tikhaya Zavod' Bay and the larger Vostok Bay in the same gulf are closer to entrapped small water bodies. Water circulation caused by a branch of Primorye current, flow from Volchanka river, and characteristics of the coastal topography ensure a high concentration of *M. trossulus* larvae in this region of Vostok Bay (Buyanovskii, Kulikova, 1984) (see P. 100).

A thorough investigation of the larval density dynamics of invertebrates inhabiting the silt floor of Mission Bay (California) revealed during a tidal cycle (of less than 2 h) a 10-fold fluctuation of larval density, i.e., fluctuations comparable to levels in different seasons and years (Levin, 1986). The same study revealed a passive larval accumulation in the entrapped portion of the bay caused by water-level fluctuations. Larvae of sea urchin *Dendraster excentricus* are distributed differently in a fjord in Vancouver island region (Emlet, 1986b). Larvae remain for a long time above the parental colonies only in some cases under certain conditions of water circulation caused by weather. In most cases, larvae are transported by currents away from the fjord.

The dispersal of short-lived lecithotrophic larvae is perhaps mainly due to turbulent diffusion which transports such larvae for distances of about 100 m (Scheltema, 1986a). According to Gibbs (1984), the long residence of the population of *Abra tenuis* bivalves in Plym River estuary (England) is probably possible due to the absence of pelagic larvae among this species which may have been transported beyond the estuarine limits.

Vertical distribution

Larvae of benthic invertebrates moving along the vertical at 1-60 cm min^{-1} may occupy and hold a position at a definite horizontal level of the water body in all regions except bodies in which there is intense water stratification (Mileikovsky, 1973b). Thus, at 10 m depth, the larval population of benthic invertebrates in the White Sea decreases sharply while they are almost wholly absent in the near-bottom layers due to significant temperature stratification of water (Shuvalov, 1978; Oshurkov et al., 1982). According to Scheltema (1986a), echinoderm larvae cannot effectively alter their vertical distribution in a natural environment due to their weak locomotory system while bivalve larvae are probably capable of actively shifting their vertical position in stratified estuaries with weak or moderate bottom currents; in estuaries with high velocities, even bivalve larvae behave like passive particles. In Posjet Bay, Sea of Japan, the maximum population of *Mizuhopecten yessoensis* larvae has been detected in the 4-8 m layer (Belogrudov, 1980) while in the shallow lagoon of Amursky Bay, Sea of Japan, *Crassostrea gigas* larvae are concentrated in the near-bottom layers at a depth of 1.0-3.5 m (Rakov, 1981).

Temperature and salinity gradients, varying concentration of edible particles at different levels, gravitational forces, and daylight gradient influence the vertical distribution of larvae. Thorson (1964) emphasized the role of the last factor in the dispersal and settling of larvae. The effect of light, including its wavelength, on the behavior and dispersal of active larvae of crustaceans is clearly manifest and has been well studied (Forward, Cronin, 1979; and others). Some examples of the effect of light on bivalve larvae follow. Larvae of *Crassostrea virginica* exposed to powerful light close their valves and descend; if the illumination remains unaltered, larvae resume swimming. Larvae perfer to gather under shade if shaded sections are available (Andrews, 1979). In Saroma Lake (Hokkaido Island), larvae of *Mizuhopecten yessoensis* find themselves at a depth of 6-12 m during the clear daytime, rise to the 0-3 m layer before sundown, disperse uniformly in the near-surface layers at night and, as the sun rises, their population in the upper layers of water diminishes gradually (Maru et al., 1973). Petipa (1955) made interesting observations in the Black Sea during the solar eclipse of June, 1954. It was found that during the eclipse larvae of benthic invertebrates rose to the surface but descended again when the eclipse ended. Larvae of scallop *Placopecten magellanicus* did not concentrate in the upper 10 m layer in Fundy Bay on the Atlantic coast of Canada but were uniformly distributed in the 40 m turbulent layer with high aggregations in the region of thermocline at depths 5-20 m; the causes of such aggregation are not known (Tremblay, Sinclair, 1988). On Georges Bank they were concentrated in the pycnocline or above it independent of food availability there (Tremblay, Sinclair, 1990; see also Raby et al., 1994). Daily migration of the larvae of *Placopecten magellanicus*, judging from laboratory data, lead them to concentrate (more than 100 times the larval density in the water column) in the surface layer at night and above the thermocline during the day; only the late larvae enter the thermocline zone and may settle on the bottom. Evidently, the water body is not homogeneous for larvae and they are concentrated in frontal zones, down- and upwellings (Gallager et al., 1996).

Under natural conditions a time-space correlation between densities of phytoplankton and larvae has been recorded (Starr et al., 1991, 1994; Pedrotti, 1993; Raby et al., 1994). It has been demonstrated in the laboratory that larval aggregation at sites of food collection is the result of their activity and not that of simple hydrodynamics (Metaxas, Young, 1998a, b).

Dynamics and density

The temporal dynamics and density of larvae in plankton depend firstly on the season and intensity of spawning which determine the recruitment dynamics to the larval pool; secondly, on the duration of the pelagic stage

and, thirdly on the loss of larvae in this pool as a result of the transport of larvae beyond the range of the water body under consideration, their settling or mortality. The season and intensity of spawning depend on diverse abiotic and biotic factors which influence gametogenesis and initiate spawning. Duration of the pelagic stage depends on the ambient temperature, availability of food to larvae and, in the late period of pelagic life, availability of a suitable substrate for settling. This last period of pelagic life of larvae is termed competent as larvae by then are capable of testing the substrate and developed to the extent of settling and undergoing metamorphosis. The whole of the preceding period of pelagic life is called precompetent: in this period, larvae grow, swim, and feed (see Scheltema, 1986a). When a suitable substrate is lacking, larvae delay metamorphosis and remain in the plankton. Precise data are not available on the extent of food availability to larvae under natural conditions (Andrews, 1979; Scheltema, 1986a). The phenomenon of facultative planktotrophy in lecithotrophic larvae of sea urchin *Clypeaster rosaceus* is interesting: in water containing food, larvae feed but, when food is not available, undergo metamorphosis without feeding (Emlet, 1986a). Facultative planktotrophy has been detected in bivalve *Codakia orbicularis* (Alatalo et al., 1984) and studied in detail in nudibranch mollusk *Phestilia sibogae* (Kempf, Hadfield, 1985).

Several experimental investigations (see, e.g., Loosanoff, 1969) have been carried out to study the effect of temperature on larval development. Field observations also suggest dependence of duration of pelagic period on temperature. For example, duration of the larval life of *Mizuhopecten yessoensis* is 22-35 days at 7-13°C (Motoda, 1977; Belogrudov, 1980) and 15 days at 17-19°C (Belogrudov, 1980).

According to Thorson (1950), larval mortality is almost on the same enormous scale as fecundity of these species. There is very little information about the mortality of larvae in nature, however. Korringa (1941) showed that the mortality of larvae of *Ostrea edulis* is 1-2.5% and likewise in *Crassostrea gigas* (Quayle, 1964) and *Mercenaria mercenaria* (Carriker, 1961). In entrapped water bodies, the daily reduction (including mortality) of larvae of *Mytilus edulis* and *M. trossulus* from plankton is 12-14% (Jorgensen, 1981; Kasyanov, 1987b). Sudden death of the larvae of oyster *Crassostrea gigas* in Hansan Bay on the Korean coast comprised 0.1-0.3 per day (Yoo, Ryu, 1985).

The natural mortality of the larvae of marine invertebrates was analyzed by Rumrill (1990). Larval mortality in plankton was high but it was difficult to differentiate from other causes of reduced population of older larvae in a given region. It has been suggested that mortality during settling signficantly exceeds that in the plankton (Morgan, 1995).

Embryos and larvae which possess less perfected mechanisms of protection from adverse environmental factors compared to the parent

organism, are generally[1] more sensitive to temperature, salinity, and other extremes (Kinne, 1970). This may be reflected in the direct death of embryos of larvae as well as decelerated development. The latter, also caused by food inadequacy or absence of suitable substrate for settling (Doyle, 1975; Strathmann, 1982), prolongs the duration of larval residence in the plankton and thus reduces the survival chances of larvae since planktonic larvae are exposed to severe pressure from predators—predatory planktonic crustaceans, fishes and benthic filter feeders (Thorson, 1950; Berg, 1971; Tregouboff, Rose, 1978; Pennigton et al., 1986). Larvae of species with lecithotrophic strategy compared to planktotrophic strategists remain in plankton for a very short duration and hence the mortality of larval cohorts of the latter species is much less. Progeny during brooding is of course in a safer state than larvae in the open sea (Emlet et al., 1987; Leven, Bridges, 1995) but the brooding conditions in the parental chambers have not been studied (Pechenik, 1999).

The above comments confirm that space-time dynamics or larvae is determined by the combined influence of abiotic and biotic environmental factors, functioning of parent populations, and characteristics of behavioral responses of larvae themselves.

Reproduction and development of planktotrophic strategists are much more dependent on the environment compared to lecitotrophic strategists. Planktotrophic strategy is cofined more to the open environment while transition to lecithotrophic strategy represents transition not only to a more economic method of reproduction, but also to reproduction which is less dependent on external factors. Embryonization of development and hence its greater autonomy from environmental factors, charts the course of progressive evolution of ontogeny (Shmal'gauzen, 1942; Zakhvatkin, 1949; Ivanova-Kazas, 1975). Transition to lecithotrophic strategy facilitates living in new habitats, especially at greater depths (Rokop, 1974), polar waters, fresh waters, and lastly on land (Kaufman, 1977).

Genetic exchange between populations

The genetic similarity between populations depends on the gene flow between them. Differences between populations are the result of differentiating selection, genetic drift, effect of heredity and presence of barriers to gene flow. Palumbi (1992, 1994) explicitly described the significantly high genetic homogeneity of populations of marine organisms in vast expanses compared to populations of terrestrial organisms. Gene

[1]Every rule has exceptions. Thus, early larvae of *Mytilus edulis* which reside normally in the surface layer of water subjected to freshening are more stable to freshening compared to adults (Yaroslavtseva et al., 1986). Larvae of oyster *Crassostrea virginica* were surprisingly tolerant to low oxygen concentrations, this being associated with insignificant size of larval body and energy metabolism based on lipids and proteins and not on carbohydrates (Mann, Rainer, 1991).

flow in sessile marine bottom invertebrates is caused by larval dispersal by currents (see p. 103). Scheltema (1986b) noticed that the terms of reproduction may have great importance for gene flow between populations since the direction of currents transporting larvae may differ in different seasons. On the Oregon coast, the transport of larvae of sea urchins *Stronygylocentrotus franciscanus* and *S. purpuratus* is associated with winter and summer patterns of currents while the return of late larvae is ensured by wind transport of water coastward (Miller, Emlet, 1997). The role of currents is particularly significant in larval transport in estuaries. As pointed out before, the current system in estuaries is usually such that late larvae return to their birth sites; this ensures the genetic stability of the local population. Larvae flowing with currents provide gene flow for other populations; larvae of other populations arriving with currents introduce an additional genetic variability in a given population. Unfortunately, no methods are available to date to distinguish local larvae from immigrants and the magnitude of gene flows in therefore not known. Recent population-genetic researches on larvae are very important in evaluating the role of larvae in gene flow between populations (Coffroth, Mulawaka, 1995; Medeiros-Bergen et al., 1995). The polymerase chain method of analysis used in recent years to study the larval genome of sea cucumbers (Olson et al., 1991), and the work of Hu et al. (1992) have initiated the study of the genome of pediveligers of some species of oysters in nature and under breeding conditions. Allozyme loci common for larvae and adults have been identified. The genetic similarity or difference between geographically separated populations of *Crassostrea virginica* and *Mytilus edulis* on the Atlantic coast of the USA (Hillman, 1964; Milkman et al., 1972, after Scheltema, 1975) has been explained by Scheltema (1975) as due to ease or difficulties of larval exchange between populations. A series of investigations by Australian biologists (Nash et al., 1988; Watts et. al., 1990; Hunt, 1993; Murray-Janes, Ayre, 1997) have revealed the role of eastern Australian current in the larval transport in bivalve mollusks and echinoderms over a distance of up to 1,300 km and thus in maintaining the genetic unity in populations of these animals. An insignficant genetic differentiation was noticed between Indo-West Pacific populations of sea star *Linckia laevigata* living thousands of kilometers apart. These observation confirm the existence of large homogeneous panmictic populations with extensive settlement in the eastern part of the Indian Ocean and western part of the Pacific (Williams, Benzie, 1996). A similar pattern was detected in sea star *Acanthaster planci* in the extensive Pacific Ocean region (Nishida, Lucas, 1988). Electrophoretic allozyme analysis of six populations of this sea star showed that the recent population explosion has a common genetic source and this source of recruitment was one and the same in 1986, 1989, and 1994 (Benzie, Wakeford, 1997).

Larval transport by currents enables formation of hybrid zones with

hybrid species of the same genus. This phenomenon has long been known in the case of mollusks of genus *Mytilus;* it has also been demonstrated for species of sea urchins of genus *Diadema* (Lessios, Pearse, 1996).

A weak larval exchange explains a low level of genetic polymorphism in bivalve populations of *Bathymodiolus thermophilis* inhabiting the deepwater thermal sources in Galapagos Rift and East Pacific Rise (Grassle, 1985).

Large-scale dispersal of larvae from estuarine colonies is an important consequence of prolonged planktonic period although larval dispersal for long distances does not offer a short-term advantage to parent populations (Strathmann, 1982). Larvae render exchange possible not only between subpopulations and populations disposed along the coast, but also with populations far removed, for example those present on the opposite coasts of the ocean. Larvae of gastropods and some other groups of benthic invertebrates in the open ocean are not a rarity but rather a common phenomenon. Such larvae possess morphological features that facilitate prolonged residence in the pelagic zone. These features are: long periostracal spines, reduction or total absence of shell calcification and signficant size enlargement of velar lobes (see p. 29). Species with such larvae fall at the end of the continuum of the ability of the progeny for dispersal. On the opposite end are species with direct development. At the center of this hypothetical continuum are species with planktotrophic strategy with larval development extending for 3-6 weeks. Larvae of these species can barely sustain transoceanic gene exchange between populations but can spread for hundreds or thousands of kilometers along the coast over several generations and intersect shallow epicontinental seas with oceanic currents. Species of mostly the latter type are studied in this book.

The distribution range of species of sessile organisms is not established and maintained by pelegic larvae alone; other mechanisms of dispersal in particular rafting—transport by floating objects, together with adult specimens by currents, broadcasting by birds and ships may determine the extent of distribution (Bhaud, 1984). Scheltema (1986, 1989) recognized four methods of dispersal of bottom invertebrates—migration of adult organisms, rafting, human transport and passive transport of plankton larvae. With the exception of sea lilies and bivalve mollusks permanently attached to the substrate, the animals under our consideration adopt, among others, the first method for enlarging the distribution range and exchange of genetic information between populations.

Rafting—transport of epibionts by means of floating objects and organisms—is widely prevalent in marine invertebrates (Highsmith, 1985). In recent decades, many organisms have begun to be transported by overgrowing on different man-made objects such as bits of plastic material, bottles, floats, nets. Rafting also includes the secondary floating of juveniles of bivalve mollusks by means of long byssus threads playing the role of

spiderling cobwebs (Sigurdsson et al., 1976). Seasonal, lunar, and 10-day cycles of drifting of juvenile mollusks from the original settlement site have been identified (Armonies, 1992).

Rafting is encountered more often in temperate waters than in tropical waters because of drifting algae transported a long time over the sea until total disintegration (Highsmith, 1985; Parker, Tunnicliffe, 1994). In the tropics, in the open sea, teleplanic larvae predominate. Among teredinids (shipworms), species extend their range energetically with prolonged brooding and transient pelagic larvae; in these species, adult organisms are transported by floating wood and their larvae rapidly colonize on the nearest substrate (Hoagland, Turner, 1980).

Among species with lecithotrophic strategy, unlike in species with planktotrophic strategy, the area is usually not large and the geological life span of the species is small. Such species rapidly perish or evolve into other species (Jablonski, Lutz, 1983). Exceptions to the rule are more interesting. Genetically subdivided population structure is absent in the African gastropod mollusk *Bullia digitalis* with lecithotrophic development culminating in the release of crawling juveniles (Grant, da Silva-Tatley, 1997). According to these investigators, there is either a gene flow of undeciphered mechanism between the populations or the geographic distribution range of this species has recently enlarged, creating the impression of a high level of gene exchange. It is generally well known that species with lecithotrophic development are comparatively short-lived but *B. digitalis* has a long history of evolution (5-20 million years) and large distribution area. Grant and da Silva-Tatley (1997) added that, in any case, the population-genetic structure of this species considerably weakens every correlation between type of larval development and population-genetic structure in gastropods. Unfortunately, information on the life span of the species is very difficult to gather. For this reason, data on the relationship between the type of reproduction and duration of existence of a given species are scant. According to Scheltema, gastropod species with teleplanic larvae survive for more than ten million years. Late Cretaceous gastropod mollusks from the Gulf of Mexico with planktotrophic larvae survived on average for six million years with a distribution range spanning 1,500 km while species without planktotrophic larvae existed for about three million years and their range extended for a length of 610 km (Jablonski, 1980). Unfortunately, data on bivalve mollusks and echinoderms are ambiguous or lacking.

The role of larvae in ensuring genetic continuity between subpopulations of marine inverbrates has been studied by Strathmann (1974b), Gooch (1975), Koehn et al., (1976), Marcus (1977, 1980) and Pudovkin and his colleagues (1981; 1998). The last of the above investigators demonstrated that various settlements of *Crenomytilus grayanus*, *Crassostrea gigas*, and *Patiria pectinifera* seen in Peter the Great Bay represent a single population.

This genetic similarity is ensured by the presence of pelagic larvae in each of these species. The duration of residence of these larvae in plankton is quite adequate for combining the different settlements in the bay into a common population. Larvae of these species, like those of other bivalves and echinoderms, are poor swimmers and their active swimming could not be accounted for when analyzing larval dispersal. Sometimes, a surprisingly high level of genetic structure of population is detected in marine species with pelagic larvae (Lewis, Thorpe, 1994). Edmands et al. (1996) state that gene flow as a result of dispersal of long-lived planktotrophic larvae presupposes genetic homogeneity of marine populations over long distances. Although many empirical data confirm this premise, there are several exceptions for various reasons. The immense potential of marine species for dispersal may not be realized due to behavioral mechanisms favoring local recruitment. Barriers restricting larval dispersal in the sea may be the force anf direction of wind and ocean currents (Palumbi, Metz, 1991; Black et al., 1995), changes of sea level, tectonic disturbances and volcanic eruptions (Avise et al., 1987; Sounders et al., 1989). Effective dispersal may be restricted by powerful currents as well as local eddies and upwellings. El Nino current fluctuations that have recently attracted attention due to their effect on climate also affect larval transport over long distances in the equatorial Pacific (Scheltema, 1988; Richmond, 1990). The "reverse dispersal" of larvae from south to north along the Californian current up to Cape Conception has in particular been explained by El Nino fluctuations (Palumbi, 1995). Another example of the restrictive effect of currents is the dispersal of larvae of sea urchin *Evechinus chloroticus*. Currents restrain larval emergence from fjords in New Zealand and limited exchange of larvae between fjords may lead to the noticed genetic differentiation of populations of this species. In the open coastal expanses, settlements of this species are genetically similar (Lamare, 1998). Similar is the pattern with the estuarine settlements of mussel *Mytilus edulis*, genetic differences between them arising due to diminished larval exchange (Corte-Real et al., 1994). Recruitment through their own larvae may explain the existence of isolated settlements of sea star *Pisaster ochraceus* (Sewall, Watson, 1993).

Genetic differentiation of populations may also proceed in spite of significant dispersal of larvae as a result of differential mortality after larval settlement and temporal variations of the genetic habit of larvae or recruitment (Edmands et. al., 1996).

Scheltema (1986b) wrote of the need to consider geographic events of the past, in particular those that may have influenced larval drift, when analyzing present-day dispersal of species. Thus, transgression and fall in sea level altered the number of suitable habitats on the coastline which served as "intermediate stations" for larval dispersal. The possibility of larval transport by currents depended on openings or closures of passages

between seas and oceans as well as widening of the ocean floor. In the latter event, enlargement of ocean basins served as a barrier for the spread of larvae of coastal species. When analyzing the distribution ranges of species, it is imperative to understand the ancient currents, for example, the westward circumtropical current passing through the Tethys Sea and the strait between North and South America. Only three million years ago, larvae traveled from the western Atlantic into the eastern Pacific through the strait between the two Americas. The find of common species on both sides of Central America is therefore not surprising.

While the genetic homogeneity of sea stars inhabiting the Great Barrier Reef (like bivalve mollusks there—Benzie and Williams, 1992) can be easily explained by contemporary distribution of larvae and the suitability of many habitats for these species (Williams, Benzie, 1993), the similarity of populations in the eastern part of the Indian Ocean and western part of the Pacific may be associated with enlargment of the distribution range (see also Palumbi, Wilson, 1990, in relation to sea urchins *Strongylocentrotus purpuratus* and *S. droebachiensis*) due to changes in sea level and temperature about 10,000 years ago after the last Glacial Epoch. Adopting such an assumption, the conclusion may be drawn that the genetic similarity of populations does not necessarily reflect the present-day settlement pattern of larvae (Williams, Benzie, 1996). Williams and Benzie detected a similar pattern in *Tridacq*. It was found that the direction of genetic exchange between the populations of *Tridacna gigas* inhabiting Micronesia, Melanesia and the Great Barrier Reef is not parallel to the main surface currents in the ocean but interesects them; probably, the genetic association of the populations of *Tridacna* coincides with the ancient currents and not with the present-day course of larval migration (Benzie, Williams, 1995). The genetic break in populations of estuarine species *Crassostrea virginica* spatially linked at present also reflects not the present-day situation with respect to larval distribution, but the picture prevailing in the period of low standing of the sea in the Pleistocene (Reeb, Avise, 1990).

To evaluate the role of larvae in the formation of fauna in the past, it is necessary to know the temperature of the ocean at which larval development took place—the greater the temperature, the more rapid development—as well as the contours of the former coastline of the ocean: at the beginning of the Tertiary period, the larvae of marine invertebrates may have crossed the Atlantic Ocean in the equatorial region in 2-4 weeks but, at present, such a crossing would need 20 weeks or more (Scheltema, 1989).

With commencement of navigation, a new method of enlargment of distribution range of the species arose, viz., by attachment of settling larvae to a ship's body. With the species attached and growing, the slow-moving sailing boats with comparatively long berthing intervals in ports influenced the distribution of marine and estuarine organisms not only on a global

scale (leading to invasion by non-indigenous species), but also to their distribution along the shelf (leading to changes in the distribution of aboriginal species). Marine transport played an important role in the gene flow between isolated populations of obligate estuarine organisms, especially those whose development proceeds without planktonic larvae. This process occured even centuries ago before the commencement of systematic marine biological investigations (Carlton, Hodder, 1995).

Recently, especially in the context of growing tanker fleets, all biogeographical maps are crisscrossed with transport of alive larvae of bottom invertebrates including echinoderms and mollusks by ballast waters of tankers over limitless expanses (Carlton, 1985, 1987; Williams et al., 1988; Carlton, Geller, 1993; Ruiz et al., 1997). A clear example of such transport is the settlement of coastal waters of Tasmania by larvae of *Asterias amurensis* from the Sea of Japan (Byrne et al., 1997). Allozyme data showed that the Tasmanian population probably arose from larvae of central Japan but not from the waters of southern Japan or the Russian coast (Ward, Andrew, 1995).

Settlement and Recruitment

Settlement

In the pelagic period, the decisive factors in larval life, barring food, are abiotic environmental conditions. For this reason, development with pelagic larvae disappears in extremely unfavorable hydrological conditons. In the period of settling, the larva tests the substrate for its physical properties such as texture, relief, color, exposure to light, and spatial disposition. According to Scheltema (1977), the foremost condition of settlement is larval response to the biological content of the substrate. In many cases, it is necessary that the substrate be covered with a bacterial-algal layer; in a laboratory culture, such data were, among others, obtained for *Ostrea edulis* (Cole, Knight-Jones, 1949), *Crassostrea virginica* (Crisp, 1967), and *Brachiodontes lineatus* (Kiseleva, 1966). This layer in other cases has no influence or even suppresses settling. L-DOPA (L-3, 4-dihydroxy phenylalanine) induces larval settling and metamorphosis in oyster *Crassostrea gigas* while adrenaline and noradrenaline induce metamorphosis. These substances are contained in the bacterial film covering oysters; they or their mimetics are released by juvenile and adult oysters (Coon, Boner, 1985).

Larvae of several bivalve mollusks and some echinoderms settle on algae and may respond not to the algal substrate as such, but to substances released by algae into the water (Kiseleva, 1966). Larvae of *Mytilus edulis* show preference to settle on *Ceramium rubrum* and *Polysiphonia* sp. of algae (Bayne, 1976b) and larvae of *Aequipecten irradians* on grass-wrack

(Sastry, 1979). Planktotrophic larvae of scallop *Mizuhopecten yessoensis*, widely distributed in the Sea of Japan, settle on extremely diverse substrates: algae *Ceramium kondoi, Desmarestia viridis, Polysiphonia* sp., *Laminaria cichorioides, Heteromorpha* sp., *Sargassum pallidum, Ahnfeltia tobuchiensis*, sea grass *Zostera marina*, hydroid *Obelia plana* and tubes of polychaete (Kasyanov, 1991). Larvae of scallop *Chalmys islandica* settle well on live hydroids *Tubularia larynx* and filamentous red algae *Ptilota phycodrys* but 20 times more intensively on dead hydroids *T. larynx* (Harvey et al., 1993).

Settling of larvae of scallop *Pecten maximus* on red algae causes their metamorphosis. Jacaranone, a derivative of tyrosine, liberated from red alga *Delesseria sanguinea* serves an inductor of metamorphosis (Cochard et al., 1989). Larvae of sea urchin *Strongylocentrotus purpuratus* settle predominantly on red algae—coralline and others (Rowley, 1987). Like the larvae of sea urchin *Strongylocentrotus purpuratus*, those of *Paracentrotus lividus* also settle successfully on red coralline algae: these algae cause 99% induction of metamorphosis. In the light of the role of bacterial film as an inductor of metamorphosis, it is important to note that the treatment of algae with antibiotics did not affect their ability to induce metamophosis (Gosselin, Jangoux, 1995). Larvae of *S. purpuratus* settle more readily on coralline algae than on rocky ground or plastic covered with a bacterial film (Rowley, 1989; Harrold et al., 1991). Larvae of *S. intermedius* and *Scaphechinus milabilis* also settle on red coralline algae, especially on *Melobesia* overgrowing on old *Zostera* grass. Glutamine liberated from *Melobesia* serves as an inductor of metamorphosis (Naidenko, 1996). Coralline algae serve simultaneously as substrate and food of juvenile sea urchins but the latters are largely eaten by crabs there (Rowley, 1989b, 1990; Harrold et al., 1991). Larvae of sea urchins *Arbacia punctulata* and *Lytechinus pictus* went into metamorphosis when settled on a substrate covered with a bacterial film (Cameron, Hinegardner, 1974). Larvae of sea urchins are usually satisfied with the bacterial-algal film commonly present in the sea as a substrate for settling (Chia et al., 1984). This substrate is adequate for the settlement of larvae of many species of sea stars, in particular omnivorous types. Larvae of sea stars *Acanthaster planci, Culcita novaeguineae*, and *Linckia laevigata* which feed on corals, settle on coralline alga *Porolithon* (Yamaguchi, 1973, from Chia et al., 1984). Larvae of sea star *Stichaster australis* settle on alga *Mesophyllum insigne* which serves as food for young of this species (Barker, 1977); tubes of polychaete *Phyllochaetopterus prolifica* attract larvae of sea star *Mediaster aequalis* whose juveniles feed on this polychaete (Birkeland et al., 1971). Interestingly, field observations suggesting the association of one species with another are inadequate for judging the preference of the first species for settling in the habitat of the second. Thus, larvae of bivalve mollusk *Mulinia lateralis* living in association with polychaete *Diopatra cuprea* settle occasionally around tubes of this polychaete and the subsequent association of the two species

is perhaps the result of differential survival (Luckenbach, 1984, from Woodin, 1986). Larvae of teredinids and wood-boring pholadids settle on dead wood (an exception is the genus *Zachsia* which settle on live rootstock of grass-wrack, (Yakovlev, 1988). In the absence of wood or its extracts, lavae do not settle, perish or delay settling, and metamorphosis by a few weeks (Turner, 1976). Culliney (1975) showed that humic material liberated from wood submerged in a river and transported by it to the sea induces settling of veligers of woodborers.

Along with those which induce settlement, there are also inhibitors of settlement and metamorphosis. For example, the Panamian *Dahlbergia* red tree liberates obtusaquinone which obstructs penetration of woodborers into the tree and causes their death: larvae deposited on *Dahlbergia* die as they cannot complete metamorphosis (Turner, 1976).

Information on the influence of adults on the settling of larvae of the same species is contradictory. For example, in soft grounds, according to some authors, with high densities of adult colonies of bivalve mollusks *Mya arenaria* and *Macoma balthica*, the abundance of settling larvae decreases (Hines et al., 1989) while, according to others, larvae collect passively in colonies of adult mollusks, crowding around their siphons (Ertman, Jumars, 1988). Wilson (1991) reached the conclusion that the present level of understanding of these phenomena does not assist in predicting the conditions under which interactions between adults and their larvae become important factors in the life of the community. However, it is known that gregarious settlement is characteristic of the larval settlement of many marine invertebrates including bivalves and some echinoderms. Under the influence of pheromones exuded by adults, larvae prefer to settle on substrate which has already been settled upon by organisms of the same species (Burke, 1986). Bayne (1969) showed that an aqueous extract of the tissues of *Ostrea edulis* and its pallial fluid placed on any surface caused larval settlement: there was no effect on settlement when the extract was simply added to the water. Thus, the settling larva needs contact with the treated surface. Veitch and Hidu (1971) clarified that the substance causing settling of *Cassostrea virginica* larvae and contained in the fluid of the pallial sinus of the mollusk is a high-molecular weight protein. This protein contains thyroxin and, perhaps, 3, 5-diiodotyrosine and 3-iodotyrosine which induce settling. Gregarious behavior is well manifest in larvae of species leading a sessile life style which, by itself, ensures further reproductive contact between organisms. Extracts of some tissues of adult sea urchin *Dendraster excentricus* cause metamorphosis of larvae of this species. A peptide with molecular weight 980 dalton isolated from extracts caused metamorphosis at a concentration of 10^{-6} M (Burke, 1984, 1986). This protein perhaps serves as an active source in inducing larval metamorphosis by water from a body which held adults and sand on which they lived (Highsmith, 1982).

Metamorphosis of young competent larvae of sea urchin *Tripneustes gratilla* is induced by a combination of algae-containing benthic film and sea water which held adults of the same species. The older competent larvae metamorphose spontaneously (Chen, Run, 1987). Adults of *Psolus chitonoides* cause gregarious settling of pentactula of this species (Young, Chia, 1972). According to Burke (1986), instances of gregarious settling of larvae of marine invertebrates in habitats of adults represent primitive variants of chemical communication among animals with the help of pheromones. Pheromones can be regarded as a special case of signals emanating from habitats preferred by juveniles or adults. Signals are perceived by surface sensors of larvae and transmitted by effectors of metamorphosis of larval and imaginal tissues. The response is a combination of morphogenetic, histolytic, and histogenic processes (Burke, 1983). Investigations on the identification of chemical inductors of the settling of marine invertebrate larvae and the mechanism of their action carried out in the 1970s-80s have been reviewed by Morse (1991) and Pawlik (1992).

Hydrological conditions influence the settling process. Settling proceeds better in water bodies with low flowing rates (Ajana, 1979). According to Rudyakova (1981), settling of *Mytilus edulis* is essentially a passive process similar to the sedimentation of inanimate particles from an aqueous layer adjoining the substrate; settling is facilitated in sections with uneven microrelief in which eddies are formed and carry the larvae closer to the substrate. While emphasizing the decisive importance of hydrodynamic processes during settling, Rudyakova pointed out that larvae present in the boundary layer gather information about the distance to the substrate from the gradient of the horizontal vector of flow velocity on the boundary layer. By perceiving this gradient, the larva probably can travel efficiently toward the substrate. Hydrological conditons of larval settlement of polychaetes in the benthic boundary layer have been analyzed by Butman (1987). Compared to the settling of larvae on hard substrates, settling on soft grounds has been rather little studied so far. Recently, the role of bottom currents transporting the larvae of infaunal animals directly above the ground has become clear. These currents assist them in surveying large areas for a suitable substrate.

For many infaunal animals, for instance bivalve mollusk *Mulinia lateralis*, a suitable substrate is silt enriched with organic matter. Larvae slowly floating above it settle and undergo metamorphosis (Butman et al., 1988; Grassle et al., 1992). For settlement of the larvae of bivalve mollusks on soft grounds, the bottom particle size is not as important as its accessibility. With increasing exposure of the ground to the larvae, the ground characteristics become less important for larval settlement (Wu, Shin, 1977). Under laboratory conditions, larvae of bivalve mollusk *Spisula solidissima* in the period of settlement are capable of actively selecting the substrate with preference for sand over silt (Sneldrove et al., 1998).

It would be terminologically useful to distinguish between the concepts "primary settlement" and "final settlement (= attachment)" of larvae. The former is determined predominantly by physical and hydrodynamic factors while the latter is associated with efficient selection of the precise site by the larva (Hadfield, 1986). According to Butman (1987), the hypothesis of passive larval settlement caused by hydrodynamic factors satisfactorily explains the collection, descent, resuspension, and transport of larvae on a large scale (tens of meters to tens of kilometers). Within these vast expanses, the actual site for settlement of larvae is determined by their active search and selection as well as minute physical processes including current variations induced by the microtopography of the sea floor.

Recruitment

The population recruitment dynamics of benthic invertebrates with pelagic larvae is a component of several factors: fecundity, success of fertilization, dispersal and death of larvae, processes of settlement and metamorphosis, and death of juveniles after settling. Not unsurprisingly, therefore, Cameron (1986a, p. 145) remarked that although many investigators designed justifiable recruitment models, there are far too many lacunae for answering the fundamental question: what represents the recruitment density and its temporal and spatial variations? These variations may play a decisive role in the dynamics of benthic communities.

Horizontal distribution

Horizontal and vertical distribution of recruitment depends on the distribution of late larvae ready for settling. This distribution in turn is largely determined, as stated before, by hydrological parameters of the water body. As larvae manifest distribution in patches because of a local combination of various abiotic and biotic factors, settling also exhibits a patchy character (Andrews, 1979). Additionally, the horizontal distribution of spat depends on the distribution of organisms of the same species that have already settled, floor topography, its suitability for settling and, in case of collectors, on the site of their disposition. In entrapped water bodies, the role of hydrological parameters is manifest most distinctly and the distribution of late and settled larvae is a partial repetition of the spread of a marker dye released in water (Andrews, 1979). It should be pointed out that collectors generally modify local hydrological conditions in favor of larval settlement.

Vertical distribution

Light exerts an additional influence on the vertical distribution of recruitment. It has, however, not been possible to identify an unequivocal

dependence of settling on the intensity of light (Andrews, 1979). On the whole, vertical distribution of recruitment corresponds to the vertical distribution of late larvae. It should be pointed out, however, that according to Dinamani and Lenz (1977) and other investigators, when larval density is high, spat ultimately occupy all suitable sections and not just the more favorable ones, irrespective of the preference for settling at a given level or collector surface. Under experimental conditions, most larvae of scallop *Placopecten magellanicus* settled at depths of 0.1 to 4m, possibly up to 10.5 m; only a few larvae settled below the thermocline at 5-9 m. In this context, the possibility of high recruitment in bottom sections adjacent to frontal zones would be interesting (Pearce et al., 1996).

Dynamics and density

Recruitment of colonies of bottom invertebrates is ensured by successful completion of three processes—supply of larvae, their subsequent settlement, and survival of juveniles in the settlement region (Harrold et al., 1991). Temporal dynamics of recruitment quite clearly depends on the temporal dynamics of late larvae. Various empirical rules have been proposed for different water bodies for determining the period of accessibility of collectors and time of settlement based on knowledge of preceding settlement patterns (Andrews, 1979). There are no universal rules for prediction of settling in a given region.

Raising the temperature within certain limits and providing a substrate accelerate larval settling. Lutz and his colleagues (1979) recorded the stimulating effect of temperature on settlement of *Crassostrea virginica* larvae. They suggested that the higher temperature of water in the tidal zone and in river estuaries may be the reason for abundant settlement in these water bodies. It should not be forgotten, however, that the pattern of currents in these sections is unique.

In the absence of a suitable substrate, larvae may delay settling (Chia, 1978; Emlet, 1986b; and others). Pechenik (1990) reviewed the data on delays in settling and metamorphosis of larvae in the absence of suitable substrate. As settling is delayed, larvae become less demanding in substrate and settling conditions and the range of acceptable substrates and settling conditons broadens considerably. Larvae of sand dollars *Dendraster excentricus* and *Echinarachinus parma* may withhold metamorphosis by 4-7 weeks. Such a delay leads to a low growth rate of settled juveniles compared to controls (Highsmith, Emlet, 1986).

Species-specialists and species with attached or sessile life style can be presumed to delay setting and metamorphosis in the absence of specific substrates compared to opportunistic and nomadic species (Chia, 1978). Based on a study of reproduction and recruitment in four species of tropical sea urchins, Cameron (1986b) found that recruitment dynamics matched

with the course of the reproductive cycle and larval residence in plankton in just one species. In the other three, the absence of such a relationship is explained by the fact that recruitment dynamics and density were usually evaluated not immediately after settling, but after some interval during which mortality of settled juveniles could have been very high.

Density of settling depends, on the one hand, on recruitment of spat by larvae and, on the other, on the death of spat as a result of attachment or death. Larvae of some mollusks, for example various species of oysters, attach only once in their entire life. Juveniles of *Mizuhopecten yessoensis* remain attached for 1.5-4 months before taking to free living. The attached stage is very brief among infaunal moving mollusks (see, e.g., Hayashi, Terai, 1964; Cummings et al., 1993; Montaudouin de, 1997).

Recruitment dynamics of *Mytilus edulis* is complicated by the phenomenon of secondary settling. Larvae settle initially on filiform substrates—algae and hydroid polyps. Spat in these substrates attain a length of 1-2 mm. The average residence is algae is about a month. Sometimes the spat overwinter on the first substrate (Seed, 1969; Bayne, 1976a). They later emerge from these reservoirs of temporary attachment into plankton and settle on available mussel banks or rocky surfaces. Promising secondary settlement sites are pits, fissures, and surface abrasions. Not only organisms which have attached after primary settling but also larvae settling for the first time settle on the rocky substrate and existing mussel banks (Seed, 1969). Detachment of the spat of *Mytilus edulis* after primary attachment is not inevitable. Since byssus threads of the same species induce settling and metamorphosis of the larvae of *M. edulis* (Eyster, Pechenik, 1987), their primary settlement under nutural conditions on mussel banks may appear final, as reported by McGrath et al. (1988) and King et al. (1990) in Galway Bay on the Irish coast. The temporal dynamics and density of recruitment are far from directly related to the course and intensity of spawning of mussels because of secondary settling. After attachment following primary settling, the spat may not reach the plankton but descend directly to the bottom (Bohle, 1971). It is interesting that spat of *Mytilus edulis* swim (drift) in water by means of byssus drifting threads which differ from the structure of byssus threads produced by the mollusk for substrate attachment (Lane et al., 1985). The phenomenon of secondary settling of spat has also been detected among other bivalves—*Cerastoderma glaucum, C. edule* (Yankson, 1986), *Macoma balthica, Solen viridis, Ensis directus, Tagelus divisus*, and others (see Butman, 1987). Following the massive primary settlement on fine-granular substrate in summer on the lower littoral section of Waddenzee off the Netherlands, juveniles of *Macoma balthica* of 1 cm length form hyaline filaments reaching up to 30 cm; having detached from the substrate, they enter the water body in winter and are carried by currents through straits of the Frisian Islands in the North Sea. There they settle for a second time in the coarse-sandy upper littoral section

and form massive settlements that constitute half of the biomass of the entire local macrozoobenthos (Beukema, de Vlas, 1989). Clearly, for bivalve mollusks, the second settlement of spat may be significant in replenishing bottom populations and enlarging the distribution range. Drifting with the help of byssus threads may be particularly important for settlement of mollusks with direct development (Martel, Chia, 1991).

The transit of juveniles into water followed by settlement has also been detected in brittle stars in the coastal waters of Belize. In some species of brittle stars, the drifting of juveniles supplements that of larvae and, in others, replaces it (Hendler et al., 1999).

The significant fecundity of planktotrophic strategists and the accumulation of their larvae in entrapped sections of water bodies may lead in "productive years", under conditions of abundant food supply and free substrate, to a significant population rise. In temperate waters, this process is particularly noticeable with a distinct seasonality of reproduction: in the warm season, the abundant settled larvae raindown on benthic populations (Thorson, 1950; Berg et al., 1987; and others). Data for *Mytilus trossulus* are interesting: in Tikhaya Zavod' Bay in Vostok Gulf in which colonies of *M. trossulus* are almost absent, its population rose in one year by 1×10^6-1×10^7 organisms in an organized 0.5 ha collector (Brykov et al., 1986). Under these conditions, the stability of recruitment of planktotrophic strategists was low. In unfavorable years, recruitment may be zero, also due to suppression of the process of gametogenesis and spawning, death of larvae, and death of settled juveniles. The prevailing view that larval mortality reaches immense proportions is probably greatly exaggerated. At the same time, en mass death of recently settled juveniles is underestimated since the young are usually estimated not directly after larval settling, but after the juveniles have attained dimensions adequate for estimation and measurement. This was convincingly demonstrated by Powell and his colleagues (1984, 1986) in thanatocoenoses of mollusks settled on soft grounds. The significant mortality of juveniles has been emphasized by Gosselin and Qian (1997).

Mortality of recruits arises for a variety of reasons. The dramatic fall in population of juveniles of marine invertebrates that have just undergone metamorphosis is largely due to their being devoured by predators (Thorson, 1961; Hunt, Shleibling, 1997). MacKenzie (1970) analyzed the causes for mortality of *Crassostrea virginica* spat. According to him, the main reasons are silting and predation by sea stars and oyster-drilling gastropod mollusk *Urosalpinx cinerea*. Other causes for spat mortality may be their better development in the same species that have settled earlier or spat of other molluskan species, as well as better development of Bryozoa. Predation and starvation are also possible. According to Andrews (1979), up to 99% of *C. virginica* spat may be eaten away by flatworms of genus *Stylochus*. More than half of settled oysters perish within the first two weeks of settling.

Subsequent mortality does not exceed 4% a week (Roegner, 1991; Baker, Mann, 1994). According to Belogrudov (1980), juvenile sea star *Asterias amurensis* settled in collectors in Posjet Bay may destroy up to 90% of *Mizuhopecten* spat. Significant recruitment differences in different years have been noticed in populations of sea urchin *Strongylocentrotus purpuratus* on the western coast of North America (Ebert, 1983) and in oysters *Crassostrea virginica* in Chesapeake Bay (Ulanowicz et al., 1980). A decade-long observation of population recruitment of sea urchin *Echinocardium cordatum* showed that recruitment was abundant only in three years and totally lacking in some years (Beukema, 1985). The bottleneck in the population dynamics of sea urchin *Paracentrotus lividus* on the Mediterranean coast of Spain occurs, in their planktonic and early juvenile periods: only 12% of the plutei survive in plankton, 0.5-0.7% of settled ones develop to a diam of 2 mm, and only 0.028% grow into mature urchins (Lopez et al., 1998). Population recruitment of bivalve mollusk *Macoma balthica* is highly erratic in Gironde estuary (France) (Bachelet, 1986). According to Bachelet, this variation could be due not so much to the obvious variations of physical environmental factors, as to biological conditions, especially competitions between macoma spat and spionid polychaetes. The presence of adults of one species in the substrate of settlement of larvae of another species may not only suppress but conversely stimulate settlement; growth of *Mercenaria mercenaria* larvae settling in large numbers was observed to accelerate in the presence of a high density of miniature bivalves *Gemma gemma* on the same substrate (Ahn, 1993a, b).

The initial low survival chances of young marine bivalves brighten when larvae settle in the immediate vicinity of adults of the same species (Cameron, Schroeter, 1980). Almost immediately after settling surviving juveniles are readily spotted nearby adults. This phenomenon explains the find of spat of Grey's mussels mainly on the byssus of adults (Kutishchev, 1976, 1977; Sveshnikov, Kutishchev, 1976) although byssus threads of *Crenomytilus grayanus* do not represent the only substrate for the settlement of larvae of this species (Selin, 1982).

The level of population recruitment does not always correlate positively with adult population and spawning intensity (Andrews, 1979; Goshima, 1982). At high population density, suppression of recruitment can be expected (Hancock, 1973). The greater the density of bivalve mollusk-filtrators *Cerastoderma edule* and *Mya arenaria*, the higher the suppression of larval settlement and restriction of population replenishment. This situation might also be a consequence of adult predation on larvae (Andre, Rosenberg, 1991; Tamburri, Zimmer-Faust, 1995). The adverse influence of high adult density on recruitment can be related to the death of settled juveniles as well as larvae ready for settling eschewing sections of the floor already occupied by adults (Williams, 1980; Levin, 1981; Woodin, 1986).

The low level of population recruitment of brittle stars *Amphiura chiajei* in western Ireland is further explained by high intraspecific competition while successful recruitment correlates directly with mortality of adults (Mundy, Keegan, 1992).

Population recruitment may not even be associated with density. Recruitment of settlement in bivalve mollusk *Spisula ovalis* is determined, according to the observations of David et al. (1997), by the spatial aggregation of larvae or passive movements of juveniles and not by settlement density.

The unstable age distribution in the population is a consequence of the instability of recruitment: in some years the population of a particular age cohort may differ sharply from that of the preceding and subsequent cohorts.

The genetic heterogeneity of bivalve settlements noticed at the microspatial level (Pudovkin, Balakirev, 1985; Balakirev, 1986) is the result of differential survival rate of juveniles as a result of natural selection acting on each successive generation and replenishing the settlement. The role of natural selection at the juvenile stage in causing genetic heterogeneity in *Mytilus edulis* was substantiated by Koehn and his colleagues (1980). Hedgecock (1982) recorded similar data for acorn barnacle *Balanus glandula*: larval cohorts from which population was replenished were genetically homogeneous and microspatial genetic heterogeneity arose as a result of systematic mortality of specific genotypes.

Reproduction

Fecundity

Fecundity is an inherent parameter in the reproductive strategy. To evaluate the state of a population, one must know its fecundity as a whole, calculated on the numerical strength of organisms of reproductive age, taking into consideration the actual and anticipated fecundity of each age group (Odum, 1975). This type of data is extremely scant in the literature. Data on individual fecundity are adequate, however. Let it be noted that species with planktotrophic strategy, which dominate in communities in terms of biomass, occupy the foremost position with respect to individual fecundity.

The dominant species with manifest planktotrophic strategy have adequate energy resources for reproduction as well as for continuing somatic growth outside the reproductive period. Species with planktotrophic strategy possessing features of fugitive r-strategy expend maximum possible reproductive effort resulting in high fecundity. Such species are small and have a comparatively brief life span. The low energy flow running through species with lecithotrophic strategy not only restricts direct consumption for reproduction, but also restricts the rate and growth limits of these organisms, which directly influence the magnitude of

fecundity. Brooding and hermaphroditism are associated with the minute body dimensions of species with lecithotrophic strategy (Heath, 1979; Strathmann, Strathmann, 1982; Strathmann et al., 1984).

Fecundity is easily regulated by gonadal processes and variations in fecundity serve as one of the mechanisms in realizing the reproductive tactics of the species (Spight, Emlen, 1976). Knowing the maximum fecundity level of a given species, the habitat conditions favorable for it in a given location can be judged from the actual fecundity level (Lapin, Yurovitskii, 1959; Rutherford, 1977). Under favorable conditions, the organisms disburse maximum available energy for reproduction (retaining that needed for performing other functions). Under unfavorable conditions, the total energy flow through the organism decreases. Depending on the amount available for reproduction, fecundity varies. The mechanism of intragonadal control of fecundity has already been described (see p. 77.)

Thus, the degree of fecundity cited by various investigators for the same species from different habitats varies widely. These differences are accentuated by divergences in the methods of estimating fecundity and the terminology adopted (see the analysis of differences in the study of fishes by Anokhina, 1969).

Although the fecundity of individuals of a given species is highly variable, variation falls within certain limits that differ from species to species. In some species, fecundity is measured in hundreds and tens of millions of eggs shed annually by the female while in others the number may be a dozen or two laid once in the female's life. Ultimately, fecundity determines the demographic pattern of the population by displacing it or holding its position in the community.

Our own data and that available in the literature regarding the fecundity of marine bivalves and echinoderms presented below, make no claim to completeness; they only suggest the degree of fecundity in the species studied.

Bivalves. Fecundity is low only in brooding mollusks with the extreme case reported for *Condilocardia* sp. bearing a single embryo (Pelseneer, 1935). Booth (1979) reported a 1 mm long mature juvenile of *Lasaea rubra* which bore two embryos, each 400 μm; fecundity is a maximum in *L. rubra* at 33 embryos (Oldfield, 1955, 1964).

Fecundity is significantly higher among mollusks with fertilization in the mantle cavity; their larvae are held for some time before being released into the ambient environment. In *Ostrea edulis* belonging to this group, fecundity is 6.5×10^4 - 2×10^6 eggs.

Fecundity is maximal in mollusks with external insemination. In genus *Crassostrea*, which is close to *Ostrea*, fecundity rises to 1×10^8 eggs (Galtsoff, 1964). Edible mussel *Mytilus edulis* can shed 12 million eggs in 15 min in some regions (Field, 1922). In functionally hermaphroditic scallop *Argopecten*

irradians which spawns once in its life, fecundity is 12-19 million eggs (Bricelj et al., 1987). Fecundity rises to 270 million eggs in scallop *Placopecten magellanicus*. Infaunal clams of *Mercenaria mercenaria* and *Mya arenaria* have a fecundity of 2-37 and 3 million eggs respectively (Langton et al., 1987).

We recorded the following values for individual fecundity of bivalve mollusks: *Crassostrea gigas* 26 million, *Crenomytilus grayanus* 11 million, *Mytilus trossulus* 3.3 million, and *Modiolus difficilis* 5.7 million eggs. A positive dependence was demonstrated between fecundity and size of individuals of the same species (Kasyanov, 1985a).

Echinoderms. Echinoderms which pass the stage of planktotrophic larva in the course of their life cycle and have external insemination possess high fecundity. Fecundity of sea urchin *Strongylocentrotus intermedius* is estimated at 30 million eggs. Yakovlev (1987) regarded this value as minimal for this species spawning many generations of gametes in a single reproductive season. Fecundity of *S. droebachiensis* is about 20 million eggs (Thompson, 1979) and of *S. purpuratus* about 9 million eggs (Leachy et al., 1981). In the latter species, along with mature eggs, $0.5\text{-}2 \times 10^6$ vitellogenic oocytes 50-80 μm diam and about 1×10^8 previtellogenic oocytes 5-7 μm diam are seen in gonads. In brooding echinoderms, fecundity runs to hundreds of eggs; e.g., female sea star *Asterina phylactica* produces up to 80 eggs (Emson, Crump, 1979), *Leptasterias polaris* up to 1,500 eggs (Himelman et al., 1982, from Lawrence, 1987), *L. tenera* up to 180 eggs (Worley et al., 1977), brittle star *Axiognathus squamata* up to seven eggs (Rumrill, 1982, from Lawrence, 1987), sea cucumber *Cucumaria curata* up to 280 eggs (Rutherford, 1977), and sea uchin *Abatus cordatus* up to 110 eggs (Magniez, 1980, from Lawrence, 1987). The fecundity of oviparous brittle stars also correlates with egg size. In *Ophionereis olivacea* with egg diam 400 μm, fecundity is 60-70 eggs. The corresponding values in *Ophiolepis paucispina* are 400 μm and about 20 eggs; *Amphiura stimpsoni* 680 μm and 3 or 4 eggs and *Sigsbeia conifera* 760 μm and 5 eggs. The picture is different in viviparous brittle stars: *Amphipholis squamata* 100 μm and 1 or 2 eggs (Hendler, 1988; Byrne, 1991).

Echinoderm species analyzed by us fall in the following order of diminishing fecundity: *Distolasterias nipon* (34 million eggs), *Asterias amurensis* (19 million eggs), *Strongylocentrotus nudus* (four million eggs), *Stichopus japonicus* (one million eggs), *Scaphechinus mirabilis* (0.22 million eggs), *Patiria pectinifera* (0.15 million eggs), *Eupentacta fraudatrix* (0.02 million eggs), *Henricia hayashi* (100-1,000 eggs). The first four species have planktotrophic larvae with distinct pelagic features. The next two also have planktotrophic larvae but pelagic features in their morphology are less pronounced. The last two species have lecithotrophic larvae.

Energetics of reproduction

An accurate estimation of energy consumed in reproduction calls for a knowledge of the total energy budget of the organism and determination of the proportion of the budget going into reproduction. The energy budget comprises the following items: C = P + R + G + U + F. Here, C is energy assimilated; P the energy expended in production of somatic tissues; R the respiratory energy; G the energy spent in reproduction; U the energy liberated in excreta and F the energy lost in indigestible food (Hawkins, Lewis, 1982).

Respiratory energy R, or the energy liberated as heat, in turn comprises the energy utilized in maintaining vital activity and the energy involved in external and internal functions (Fuji, 1967). Energy distribution in reproduction and somatic growth varies over the year and usually correlates with reproductive or gonadal cycle (McDonald, Thompson, 1986; Peterson, Fegley, 1986; and others).

The allocation of energy budget for reproduction is called the reproductive effort (RE). Its analysis is important when studying the evolution of life cycles and dates back to concepts clearly expounded by Fisher (1930) for the first time. In an ideal case, RE is regarded as the proportion of assimilated energy expended in reproduction. Such data are scant in the literature. Data which are close to the concept of gonadal index, i.e., estimation in calories of the proportion of energy contained in gonads in relation to the energy contained in the organism, are more common and easier to obtain. To determine the caloricity of the tissue, it is burnt in a bomb microcalorimeter. Another method is oxidation of the tissue with a bichromate, followed by estimation of caloricity from the amount of oxidized organic matter. Such data can be obtained before and after spawning and, using them, the energy lost by the organism in the form of gametes can be determined. Another group of data pertains to the energy content of eggs. By using this information and knowing the fecundity, the overall energy consumed in reproduction can be easily calculated. Further, it is important to remember that egg dimensions and their energy content are not directly related (Turner, Lawrence, 1979; McClintock, Pearse, 1986). According to Thompson (1984), it is not quite clear at present to what extent the empirical studies on RE will be useful in developing the theory of life cycles although they are necessary for understanding the distribution of resources under diverse ecological conditions and therefore represent a useful descriptive tool. Thompson has shown that under relatively unfavorable conditions, somatic production and production of gametes fall in sea urchin *Strongylocentrotus droebachiensis* although RE rises. A similar picture is perceived in *Mytilus edulis* under conditions of moderate stress experienced by the population.

Bivalves. In bivalve mollusks-filtrators, phytoplankton serves as the main source of food and energy. The density dynamics of phytoplankton caused by seasonal fluctuations of environmental factors determines the supply dynamics of nutrient reserves for sustaining the all-round molluskan activity including gametogenesis. Nutrient reserves for gametogenesis in bivalve mollusks are stored initially in the mantle folds, digestive gland or the adductor muscle. The reproductive potential of a mollusk can be judged from the quantity of, say, glycogen (basic material reserve in bivalve mollusks and many other marine invertebrates (Hummel, 1988) in the muscle of scallop *Placopecten magellanicus* before spawning and after (Gould et al., 1988).

Having discussed the problems of energy consumption among bivalves, Lucas and his colleagues (1978) and Lucas (1982) pointed to difficulties associated with estimating the energy utilized in reproduction. Ignoring the organic matter content of the shell could be a major lacuna in estimates of enegy consumption; although the proportion of ash in shells, for example of gastropod mollusks of genus *Conus* reaches 98%, the energy content of the shell is about 33% of the total energy content of the mollusk due to its large shell weight (93-96% of dry mass) (Perron, 1982).

Lucas and his colleagues showed that the gonadal-somatic index, GSIcal, reaches 173% (repeated spawning during the year and total fecundity of about 10 million eggs) in female *M. edulis*; in less prolific *M. platensis* (fecundity about three million eggs), it is 22%. In scallop *Chlamys opercularis*, 12-21% (hermaphroditic species with fecundity about five million eggs); *Ch. tehuelcha* (also a hermaphrodite with fecundity about 10 million eggs), 11-15%. In females of oyster *Ostrea edulis* (protandrous successive hermaphrodite, larviparous and fecundity about two million eggs), the GSIcal is 12%; *O. puelchana* (species with similar characteristics and fecundity about 2.5 million eggs), 56%. The species studied by the above investigators can be arranged in the following diminishing order or GSIcal: *M. edulis* > *O. puelchana* > *M. platensis* > *Ch. opercularis* > *Ch. tehuelcha* > *O. edulis*. The series stands as follows with respect to fecundity: *M. edulis* > *Ch. tehuelcha* > *Ch. opercularis* > *M. platensis* > *O. puelchana* > *O. edulis*. The following is the sequence according to the overall caloricity of gametes shed per 100 individuals: *M. edulis* > *O. edulis* > *O. puelchana* > *Ch. tehuelcha* > *Ch. opercularis* > *M. platensis*.

These investigators came to the conclusion that, in species with K-strategy, energy consumption in reproduction is less (for example, in *O. edulis*) than in species with r-strategy (for example, *M. edulis*). Another important conclusion is that fecundity, GSIcal, and total caloricity are not interchangeable for evaluating the reproductive effort. The above series shows that there are species which expend much energy in reproduction in absolute as well as relative terms (*M. edulis*) while in other species, relative expenditure in reproduction is more but absolute values are not

high (*M. platensis* and *O. puelchana)*; a third category reveals high absolute values for a small proportion of energy expended in reproduction (*Ch. tehuelcha*). On comparing these variants with fecundity, it will be seen that species with signficant fecundity are characterized by high absolute values of the overall caloricity of gametes (*M. edulis*).

Bayne and his colleagus (1983) estimated the RE for *M. edulis*. This value varied by an order in different habitats. An example of populations with conditions to energy redistribution in favour of reproduction is the population of *Mytilus edulis* in the Baltic Sea where predatory pressure is negligible and calcium concentration in water low; as a result, the shell of these mollusks is relatively thin and the adductor relatively weakly developed (Kautsky et al., 1990). With age, the RE of *M. edulis*, as also in other organisms (Pianka, Parker, 1975), rises from nil to 40-80%. The index of the cost of reproduction (ICR)[1] at most ages is negative. i.e., gametogenesis does not proceed at the expense of energy needed for maintaining somatic tissues. However, at the oldest ages the ICR is greater than zero, i.e., gametogenesis proceeds at the expense of the total energy consumed by the organism (Bayne et al., 1983). This is because, with age, metabolic efficiency drops and, at the limit level, material and energy resources are not adequate for reproduction (Vahl, 1981).

In the population of scallop *Placopecten magellanicus* on the east coast of Canada, RE increases steadily with age and follows the temperature rise and food availability; further differences are noticed in different populations in lipid content of oocytes, proportion of nonreproducing young, and proportion of energy going into reproduction (Claerbought, Himmelman, 1996). Differences in lipid content of oocytes of *Placopecten magellanicus*, relative to habitat conditions (Napolitano et al., 1992), exert a maternal effect on larval development in culture, which in late larvae is superimposed by the feeding conditions of larvae (Stromgren, Nielsen, 1989).

In scallop *Ch. varia*, the RE measured as GSIcal varies in different years from 4 to 10% (80-800 cal specimen^{-1}). As in *M. edulis*, the older organisms spend more energy: at 0-1 year of age RE = 0.014-0.07; at four years, 0.05-0.19 (Shafee, Lucas, 1980). A similar picture has been reported for *Chamys islandicus* and *Mizuhopecten yessoensis* (Fuji, Hashizume, 1967; Sundet, Vahl, 1981). The total weight of gametes shed by 1-, 2- and 3-year-old *M. yessoensis is* 0.28, 2.35 and 5.15 g respectively. The proportion of energy going into gonadal development comprises 2% of total energy intake in 1-year-olds, 7% in 2-year-olds, and 12% in 3-year-olds. Fuji and Hashizume calculated

[1] $ICR = 1 - \frac{Ce - P_r}{R'}$. Here, C is the food ingested, e the feeding efficiency, P_r the energy consumed in reproduction, and R* the energy required for maintaining somatic tissues.

the energy assimilated as the sum of the energy of products liberated, energy expended in growth, energy of muscular work, and energy spent in maintaining the vital activity of the organism (Fuji, Hashizume, 1967). In *Placopecten magellanicus*, gamete production increases continuously with age while somatic production rises up to the fifth year and falls later or the rise decelerates (McDonald, Thompson, 1985; Langton et al., 1986). Contradictory data were reported for other species of scallops: in *Chlamys islandica*, as the shell attains a height of 80-85 mm, gonadal output drops; in *Argopecten irradians* which spawn once or twice in their life, fewer gametes are released in the second spawning (Bricelj et al., 1987). Compared to long-lived scallops, pectinids with low longevity invest a relatively small proportion of energy in reproduction (McDonald et al., 1991).

Utilization of energy in reproduction among prosobranch bivalve mollusks of *Nucula turgida* constitutes about 85% of that expended in producing somatic tissues or 47% of total production (Davis, Wilson, 1985). According to Davis and Wilson, the high RE of *Nucula* is associated with the high lipid content of eggs of this mollusk with lecithotrophic larva. In *Macoma balthica*, which cease growing after maturation, the entire energy which may have gone into growth is expended in gamete production (Gilbert, 1973).

Energy consumption in reproduction in male *Chlamys varia* is roughly 10% less than in females (Shafee, Lucas, 1980); similar data have been recorded for *Ch. islandica* and *Mytilus edulis*. Among *Aulacomya ater*, *Choromytilus meridionalis* and *Placopecten magellanicus*, utilization in reproduction is the same in males and females (McDonald, Thompson, 1986). In functional hermaphrodite *Argopecten irradians*, dry decalcified weight of male and female gonads is the same (Bricelj et al., 1987). This is in conformity with the hypotheses of Williams (1966) regarding the equal distribution of energy in male and female gametes in functional hermaphrodites.

Sea stars. By comparing the reproductive expenses among sea stars with different types of development, Menge (1974) concluded that *Leptasterias hexactis* with low (about, 1000 eggs) fecundity and *Pisaster ochraceus* with a fecundity of about 40 million eggs and planktotrophic larva spend about 9-10% of their own weight for reproduction. In *L. hexactis*, weight loss of pyloric appendages during the "incubation" of sea star brood was taken into consideration along with gonadal weight loss. Menge concomitantly showed that consumption in terms of calories in *L. hexactis* can be higher since the caloricity of one ovary of *L. hexactis* is roughly 1 kcal more than that of *P. ochraceus*.

Menge's data on energy expenditure for reproduction in *P. ochraceus* in different habitats are important for discussing the role of energy in tactical variants of reproductive strategy. In habitats insulated from waves, *P. ochraceus* expends 1,066 cal g^{-1} body weight in reproduction; in sections

exposed to waves, the consumption is 834 cal g^{-1} body weight (Menge, 1974).

Continuing Menge's investigations, we assessed the energy expenditure in reproduction in sea stars *Asterias amurensis* and *Patiria pectinifera* which differ distinctly in reproductive strategy (Kasyanov et al., 1985). Both species expend a similar proportion on gonads: 12-14% of total energy content of the animal body. In the case of much smaller *P. pectinifera*, however, the absolute values of reproductive expenditure are much less than in *A. amurensis*.

In brooding sea star *Pteraster militaris*, nutrients are supplied from the mother organism not only in the period of vitellogenesis, but also in the course of brooding juveniles in the aboral chamber of the mother. This is supported by data on energetics (energy content of eggs 10.2 J and in juveniles under brooding 54.2 J) and histological observations (digestive system processing the material of envelopes and other tissues of the mother organism that has undergone hyperplasia, functions in the young under brooding). The other sources of energy are the aborted embryos and dissolved organic matter (McClary, Mladenov, 1990).

Sea urchins. Lane and Lawrence (1979) point to the low caloricity of tissues of *Mellita quinquesperforata* and low absolute consumption for reproduction in this sea urchin compared to others. The insignificant gonadal production is the result of the fact that the space available for gonadal development is extremely restricted in sand dollars. Therefore, *Strongylocentrotus intermedius* for example, may spend 5-15 g dry weight during spawning and *M. quinquesperforata* less than 0.6 g dry weight.

In tropical sea urchin *Diadema antillarum*, the gonad contains 5,410 cal per g dry decalcified gonadal weight (760 cal ml^{-1} gonad). Hawkins and Lewis (1982) determined the caloricity per ml of gonad and, using it, calculated the energy utilized for reproduction from differences in gonadal volume before and after spawning. This sea urchin spawns twice a year. During the first spawning, 21.2 cal is liberated in the form of gametes by an urchin with test diam 20 mm and 776.6 cal by another of test diam 60 mm; these values after second spawning are 48.5 and 1,315.8 cal respectively. Thus, by calculating the mean monthly loss of energy in reproduction, the investigators showed that expenditure on reproduction occupies the penultimate position in the energy budget (R > F > P > G > U, see p. 125). The total energy consumed for reproduction and development is about 9% of the total energy assimilated (Hawkins, Lewis, 1982).

In sea urchin *Strongylocentrotus intermedius* inhabiting the Sea of Japan, Fuji (1967) determined the loss of gonadal dry weight during spawning in 1-, 2- and 3-year-old individuals and using data on percentage content of lipids, protein, and carbohydrates in gonads, estimated the total caloricity of gametes shed by organisms at different ages. In the overall energy budget,

expenditure on gonadal development is about 7% of total energy supply to the organism among 1-4-year-old individuals. Released gametes account for 4.5% of absorbed energy in 1-year-olds, 4.6% in 2-year-olds, and 3.8% in 4-year-olds. The proportion of expenditure on growth decreases with age: 12% in 1-year-olds, 3.9% in 2-year-olds, and 1.7% in 4-year-olds. Thus, after attaining sexual maturation (after the first year), much of the accumulated energy is used up not for growth of the somatic tissue but for gonadal development (Fuji, 1967). .

Reproductive effort and reproductive strategy

When studying the strategy and evaluating the possible selection of one or the other strategy or tactics by the organism, the expenses incurred by the organism in different variants of reproduction need to be estimated (Fisher, 1930; Hirshfield, Tinkle, 1975). All diverse morphological adaptations for reproduction can be expressed in economic terms that are common for all organisms. The explanation of the diversity of morphological structures in terms of their varying caloricity will, however, be as unsatisfactory as explaining the diverse cerebral functions as due to differences in oxygen concentration in the blood supply to the brain (Lidicker, 1978, from Estes, 1979).

Data on the relationship between magnitude of reproductive effort and nature of development are of interest. Christiansen and Fenchel (1979) and Kolding and Fenchel (1981) postulated the absence of a relationship between reproduction expenditure and nature of development and opined a definite evolutionally stable value of reproductive effort common to different types. Data for gastropod mollusks can be taken as a confirmation of these conclusions (Grahame, 1977, 1982; De Freese, Clark, 1983).

Following analysis of data for bivalve mollusks, Lucas and his colleagues (1978) came to a different conclusion: in species with K-strategy (for example, *Ostrea edulis*), the proportion of expenditure in reproduction is less than in species with r-strategy (for example, *Mytilus edulis*). Browne and Russel-Hunter (1978) demonstrated the high expenditure incurred in reproduction among semelparous mollusks compared to expenditure in a single spawn of *iteroparous* mollusks. A comparison of gonadal production in *semeparous* hermaphrodite *Argopecten irradians* with the corresponding value in *iteroparous Chlamys islandica, Ch. varia,* and *Placopecten magellanicus* confirms the conclusion drawn by Browne and Russel-Hunter (see Bricelj et al., 1987).

Our results (Kasyanov et al., 1985) as well as those of Menge (1974) on sea stars can be interpreted as a confirmation of the premises of Christiansen and Fenchel (1979) about a fixed value of reproductive effort in organisms with diverse reproductive strategies within a definite taxonomic group; absolute reproductive inputs are more, the greater the

manifestation of planktotrophic strategy. Reproductive cost among echinoderms with lecithotrophic strategy may vary quite significantly among species with different functional morphologies caused by differences in method of feeding and body structure of the organism. These differences render testing the hypothesis on the evolution of planktotrophic and lecithotrophic strategies based on energy consumption data difficult (McClintock, Pearse, 1986). Evaluations of reproduction expenses in Antarctic sea stars with lecithotrophic development and those of temperate and tropical waters with planktotrophic development are similar (McClintock, 1989) but a straight comparison of reproductive expenses is not of much importance due to diverse body forms of sea stars (Lawrence et al., 1984; McClintock, Pearse, 1986) and hence does not contradict the interesting hypothesis concerning the low reproductive expenditure in polar marine invertebrates due to low level of metabolism and limited access to food (Picken, 1980; Clarke, 1987).

According to Strathmann and Strathmann (1982), unlike species with small body size, those of large size do not brood because they produce a larger number of embryos cells than they can brood (production of embryos is a function of body volume and brooding a function of body surface). It should also be borne in mind that the large egg size, characteristic of organisms with lecithotrophic strategy, is not necessarily associated with high expenses in the production of a single offspring. McClintock and Pearse (1986) confirmed that concepts of Lawrence and his colleagues (1984) about the insignificant fall in amount of energy in the course of lecithotrophic development and the possible role of large egg size in producing large-size juveniles compared to those of species with planktotrophic larvae. The large size of juveniles of lecithotrophic strategists enhances their survival chances since the danger of being devoured is reduced and the prospects of seeking food (Hines, 1986), which compensates for the low fecundity of such species, brightens. Thus, among brittle stars as well as in the genus of sea star *Patiriella,* juveniles growing in brooding species with low fecundity are larger in size than juveniles of closely related species with pelagic larvae (Hendler, 1991; Byrne, Cerra, 1996).

Let us study the evolutionary aspect of one of the hypothetical mechanisms of evolution of planktotrophic strategy of reproduction and its replacement by lecithotrophic strategy in the context of the energy expended in reproduction (Kasyanov, 1981). Selection under conditons of ecological vacuum with unrestricted (although temporary) trophic resources, i.e., r-selection, will promote an increase in energy expenditure by the organism embarking on reproduction. Such is selection when settling in new, rich trophic regions and selection is temperate latitudes with seasonal variations of food availability; it promotes high fecundity leading to rapid occupation of temporary habitats by the settling broods. Opportunistic

species with characteristic fluctuations of population and especially separate settlements originate and persist in this manner (Southwood et al., 1974; Moore, 1978). Selection under relatively stable conditions in an environment already saturated with organisms results in a reduction of expense in the reproductive process. Thus, specialist species with relatively constant population strength arise under the influence of K-selection (Pianka, 1970; Moore, 1978). Crisp (1974) and Strathmann (1975a, b) emphasize primarily the variability of habitat conditions for bottom invertebrates in time and space as a factor which determines selection of reproductive strategy. In fact, reproduction with pelagic larva is characteristic of most species of bottom invertebrates in the shelf zone of temperate waters with seasonal variation of environmental factors. This type of reproduction is also characteristic of the equatorial region. Thus, it is not the instability of conditions alone that determines selection of the reproductive strategy.

Planktotrophic strategy is characterized by high and varying level of larval mortality, especially of settled young. It leads to selection of a long life span of parent organisms and repeated reproduction (Wilbur et al., 1974) while maintaining high fecundity. A long life span and iteroparity are promoted by the significant size of the organisms but then this does not enhance the efficiency of production (Humphreys, 1979); hence expenses on growth and survival of the organism should also be high (Schaffer, 1974a). On the whole, such a reproductive strategy as planktotrophy, which is uneconomical energy-wise, may be suitable only for opportunistic species with a generally high level of energy metabolism (Menge, 1975; Chia, 1974). A changeover from planktotrophic to lecithotrophic strategy leads to a better reproduction economy although the advantages of dispersal are lost (Hartnoll, 1977; Hermans, 1979). Planktotrophic strategy is particularly characteristic of dominant, widely distributed species. Lecithotrophic strategists can often be found among secondary species of different communities, species with a lower level of energy metabolism.

It must be emphasized in conclusion that the energy approach alone, however promising and important it may be, is not adequate to explain all the diversities and evolution of reproductive strategies (see also Strathmann, 1986).

Environmental factors and reproduction

Analysis of the influence of several, primarily abiotic factors of environment on reproduction and development of marine invertebrates in general and bivalves and echinoderms in particular, has attracted the attention of many investigators of the reproduction of marine invertebrates. Thousands of publications have dealt with such an analysis. Here I wish to restrict myself to a few remarks on the problem of demarcation of planktotrophic and

lecithotrophic reproductive strategies. Environment influences the annual gonadal cycle, any time, including gonial reproduction, growth and maturation of gametes (Kanatani, 1975; Lubet, Mathieu, 1982; Motavkin, Varaksin, 1983). The effect of environment is particularly perceptible at the boundary of the distribution of species (Nichols, Barker, 1984). Under the influence of environment, the duration of the gametogenetic cycle may increase or decrease, spawning may repeat within a reproductive season or, conversely, reproduction may cease (Gonor, 1973a, b). Food is the most important factor of the environment to influence reproduction. The fecundity of organisms drops abruptly, gametogenesis ceases, and gametocytes are resorbed in the absence or inadequacy of food (Bayne, 1976b; Sastry, 1979). Food shortage in abyssal (more than 100 m) settlements of scallop *Placopecten magellanicus* on the Atlantic coast of the USA, compared to shallow-water settlements, results in a fall of fecundity, resorption of germ cells, low-grade spawning and, as a consequence, inadequate recruitment of parental settlements (Barber et al., 1988). In iteroparous organisms, under conditions of hunger, material and energy supply for reproduction is "cut off" and all resources utilized for sustaining vital activity (Boolotian 1966; Bayne, 1967b; Sastry, 1979; Himmelman, 1984). It was demonstrated under controlled conditions that qualitatively and quantitatively adequate feeding accelerates the onset of sexual maturity, boosts growth, increases production of germ cells, and enhances the survival rate of juveniles and adults of sea urchin *Strongylocentrotus droebachiensis* (Meidel, Shleibling, 1999).

In the context of the role of biotic factors—presence of food, predators and competitors—the role of parasites should be recalled. The castration syndrome prevalent in different groups of organisms infected with parasites was also common in the groups studied by us. Thus, parasitic infusoria *Orchitophyra stellarum* causes 85% reduction in gonad size in male sea star *Asterias vulgaris* (Claereboudt, Bouland, 1994).

It has become clear in recent years that the gonadal cycle in marine invertebrates, as in terrestrial animals, is subject to photoperiodic regulation. Sea stars have an endogenous rhythm of reproductive processes which is set during early ontogenesis. Photoperiodic variations modify the gonadal cycle of sea stars without directly influencing gametogenesis. Sea urchins probably do not possess such an endogenous rhythm and photoperiodic control in them is more distinctly manifest: the distribution of resources between somatic development and gametogenesis depends on the duration of day light (Pearse, Earnisse, 1982; Pearse, Walker, 1986; Pearse et al., 1986a, b; Pearse, 1987). Even insignificant changes in photoperiodic conditions shift the gametogenic cycle in sea urchin *Eucidaris tribuloides* (McClintock, Watts, 1990). In sea urchin *Centrostephanus rodgersii*, it is not the temperature but changes in daylight duration and lunar cycle that determine the period of onset of spawning (Byrne et al., 1998). Holding sea

urchins *Strongylocentrotus droebachiensis* under conditions of abundant food and photoperiodic conditions favoring intense gametogenesis in nature, greatly accelerated the processes of nutrient concentration in the gonad and gametogenesis (Walker, Lesser, 1998). Photoperiodic changes probably influence the intensity of mitosis in gametogenic cells, directly as well as indirectly, as a result of intense nutrient supply to these cells (Walker, Lesser, 1998; Walker et al., 1998).

Temperature, another of the most important environmental factors undoubtedly influences the rate of nutrient supply to the gonad and the intensity of gametogenec processes (Sastry, 1979; Spirlet et al., 1998; and many other works). As in the case of other organisms, temparature requirements of the stages of the gonadal cycle can be expressed in terms of degree-days. *Ostrea edulis* on the west coast of Ireland requires 554.5 degree-days for completing the entire cycle (Wilson, Simons, 1985). In *Mytilus edulis*, some investigators have found a relationship between duration of reproductive cycle and quantum of degree-days received by the mollusk (Bayne, 1975) while others dispute such a relationship (Newell et al., 1982; Podniesinsky, McAlice, 1986). Investigations into the reproduction of bivalve mollusk *Modiolus modiolus* in different parts of its distribution range showed that the average quantity of late oocytes is more, the narrower the annual temperature range of water; spawning duration is more prolonged, the greater the degree-days received by the mollusk during the year (Browne, 1984).

In temperate waters, the brief period of high summer temperature is utilized for spawning and embryonic and larval development while gametogenic and other processes in the gonad may shift toward the less favorable, colder period of the year. A comparison of the dynamics of the proportion of species present in the gametogenic period of the gonadal cycle with the course of temperature in Vostok Bay showed that gametogenic processes proceed at a low temperature (Kasyanov, 1985a). It does not follow, however, that a low temperature is required for gametogenic processes: it only means that in the more favorable period of the year, more vital events and those involving greater risk, such as spawning and embryonic and larval development, occur. In our view, it is hardly correct to detemine the temperature requirements of different stages of gametogenesis from the data on temperature at which these stages proceed (Kaufman, 1977; Walker, Lesser, 1998). Gametogenesis ceases under conditions of extreme temperatures (too high or too low). Under favorable temperature conditions, differences in gametogenic cycles are determined by other factors, primarily trophic (Lubet et al., 1986). The high response of gametogenic processes to environmental factors is of course combined with genetic control and genetic differences of populations and individual level of the extent of fecundity and other reproductive characteristics (Hilbish, Zimmeman, 1988; Gardner, Skibanski, 1990).

The period of gonadal cycle, i.e., spawning, is most sensitive to environmental factors. Spawning (in oganisms ready for it) may be caused by diverse types of factors which are correlated with successive manifestation of target, final conditions and ensure successful embryonic and larval development, metamorphosis and settling (Giese, Pearse, 1974; Mileikovsky, 1977; Kasyanov et al., 1978; Falk-Petersen, Lönning, 1983; Koshelev, 1984). The annual variations of conditions in the period of accumulation of food for gametogenesis and in the reproductive period lead to differences in the periods and intensity of spawning in a given population or settlement in different years (Kasyanov et al., 1980; Langton et al., 1987). According to Todd and Doyle (1981), selection of the reproductive strategy (presence or absence of planktotrophic stage) among nudibranch mollusks is perhaps set by the optimal (for survival) time interval between spawning and larval settling.

Organisms whose eggs contain less nutritional material need additional energy supply for completing the stage of migrant larva and undertaking metamorphosis (Crisp, 1974; Jespersen, Olsen, 1982; and others). This energy is provided by active feeding of the larva itself . We detected a correlation between the number of larval plankton and phytoplankton as a whole in Vostok Bay. The coefficient of correlation according to Spirmen (Snedekor, 1961) is 0.44 which is statistically relevant at 5% significance. The correlation coefficient between the number of larval plankton and flagellate algae was 0.53 from the scatter of points caused by the winter spurt of flagellates. Thus, spawning of invertebrates (particularly among bivalves and echinoderms) with planktotrophic larva in Vostok Bay proceeds in the period when food suitable for lavae is abundant (Kasyanov et al., 1980). These data confirmed that compiled by Thorson (1946, 1950), Ockelmann (1958), and Himmelman (1975, 1981).

Clearly, the availability of phytoplankton is a target factor for spawning, i.e., serves for successfully achieving the objective of spawning (Baker, 1938; Giese, Pearse, 1974), but it may also act as a direct stimulant to spawning by causing it in organisms ready for reproduction (Miyazaki, 1938; Himmelman, 1981). Recently, Himmelman et al. succeeded in confirming a direct relationship between spawning of invertebrates and growth spurts of phytoplankton and isolated the substance inducing spawning from diatomic algae *Phaeodactilum triconutum* (Starr et al., 1990, 1992). Such a correlation between spawning and growth spurts of phytoplankton is not always confirmed however (Bonardelli et al., 1996). A positive correlation with a time interval of a few months was detected between the quantity of primary productivity and abundance of larvae of sea urchin *Paracentrotus lividus*, realized possibly through bacterial or heterotrophic linkages of the trophic chain (Lopez et al., 1998). Microalgal cultures have also been used to induce spawning among bivalves (Brease, Robinson, 1981; Smith, Strelow, 1983). Other direct inductors of spawning are changes in water temperature

(Mileikovsky, 1970, 1981; Giese, Pearse, 1974; Koshelev, 1984; Maksimovich, 1985; and others), extent of daylight (Cameron, Fankboner, 1986) and lunar phase (Mileikovsky, 1970; Giese, Pearson, 1974). The last event can induce spawning by desiccation of organisms during low tide (Emlet, 1986b).

For organisms living under conditions of significant fluctuations of salinity, its variations in the spawning period may constitute a decisive factor in spawning (Mileikovsky, 1981; Natarajan, George, 1983; Joseph, Madhyastha, 1984). Evidently, in different regions and for different species, diverse types of factors may cause spawning among oganisms ready for it when these factors are generally associated with the successive manifestation of conditions which ensure successful embryonic and larval development, metamorphosis and settling (Kasyanov et al., 1980). Abrupt weather fluctuations such as storms, typhoons, and cloud bursts during the reproductive season enduce en masse shedding of gametes, which is not always conducive to manifestation of larvae in the plankton: this is yet another restraint in the dependence of reproduction of planktotrophic strategists on external conditions.

Aspects of the dependence of spawning on temperature, proof for and against Orton's rule (Orton, 1982), and problems of so-called physiologically resproductive races relative to temperature have been thoroughly studied by Mileikovsky (1981) and there is no need to review them afresh. Genetic aspects of physiologically reproductive races have been dealt with by Hedgecock (1982). It may simply be mentioned that the dependence of spawning on temperature and other factors is primarily characteristic of species with planktotrophic strategy. Thus, planktotrophic larvae of bivalve *Tellina tenuis* are seen in plankton at a temperature which ensures maximum specific growth rate (Barnett, 1985). Maximum density of mytilid larvae is seen in the White Sea in the period of maximum growth rate (Beer, Plotnikova, 1988).

The level of temperature at which spawning commences in a given species depends on its biogeographic affinity (Golikov, Skarlato, 1972; Mileikovsky, 1981; Skarlato, 1981) although this relationship is far from universal (Kennedy, Krantz, 1982; Zhirmunskii, Nesis, 1983).

According to our data, boreal species begin spawning in Vostok Bay at an average temperature of +14°C, low-boreal species at +13.6°C and subtropical-low-boreal species at +18.4°C. On the whole, however, biogeographic affinity is not an important factor in determining the spawning period and spawning of bivalves and echinoderms occurs in the same periods (June-August) in Vostok Bay, which are favorable for subsequent, larval development, irrespective of species biogeographic affinity (Kasyanov et al., 1974, 1978). Kulikova (1979) came to similar conclusion in her study of the reproduction of bivalve mollusks in Busse lagoon in the Sea of Okhotsk.

For sea urchins of different biogeographic origin inhabiting the coast of Japan, the temperature at which spawning occurs corresponds to the optimum temperature range of embryonic development (Fujisawa, 1989; Fujisawa, Shigei, 1990). The observations of Fujisawa and Shigei (1990) as well as Guidice et al. (cited by Sconzo et al., 1986) about the shift of temperature optimum for development of sea urchins at the end of the spawning period are of interest. These authors explain the shift by synthesis (before spawning) of thermal shock proteins in the last portions of oocytes, noting that these proteins influence the subsquent tolerance of embryos to temperature.

Sinkage of warmer waters to the bottom is favorable to fertilization and early development, thereby inducing spawning in scallop *Placopecten magellanicus* (Bonardelli et al., 1996).

The rapid course of the larval stage is an important conditon for successful development with planktotrophic larvae since delayed development, especially when due to low temperature, increases larval mortality due to predatory attacks (Thorson, 1950). A comparison of variation dynamics in proportion of species setting out to spawn with variation in temperature of surface water layers in Vostok Bay showed a significant correlation between these curves. A correlation was also found between variation in proportion of species entering into spawning and the dynamics of other environmental factors prevailing in Vostok Bay, viz., duration of daylight including the twilight period; number of calm days in a month; and number of days with south and southeast winds which prevent larval transport into the open sea. The maximum values of these environmental parameters promote reproduction. A positive correlation was found between the proportion of reproducing species and the amount of precipitation and a negative correlation with salinity dynamics caused by simultaneous high temperature and period of rains under summer monsoon. On the whole, the set of favorable biotic and abiotic conditions in the summer season ensures successful reproduction of bivalves and echinoderms inhabiting Vostok Bay (Kasyanov, 1985a).

Data on en masse reproduction of invertebrate species in the Irish Sea correlated with periods of coastward winds and high temperature (Minchin, 1992), also accord with our data.

The study of the effect of lunar cycle on spawning in marine animals, including mollusks and echinoderms, an extremely interesting and difficult task, raises more questions than answers. Firstly, the relationship between reproduction and lunar cycle has not been confirmed in all marine animals and its absence is totally independent of the geographic region under study or the affinity of the species to a particular phyletic branch (see data on sea urchins on the coast of Central America, Lessios, 1988, 1991; Levitan, 1988). Secondly, in cases when such a relationship does exist, it is not clear which factor of the lunar cycle is responsible for it—change of nocturnal light,

magnitude of tides, desication, temperature variation in the tidal cycle or some other factor. Even if it is possible to isolate this factor, it may be specific to a given species and need not necessarily affect the behavior of other species (Lessios, 1991). Thirdly, it is not clear whether such a factor is adaptive and, if so, what objective it pursues: for example, survival of offspring as a result of their displacement from the spawning ground or if the lunar cycle serves to synochronize the processes of reproduction, and spawning in particular, in settlements of animals in reef shelters (Robertson et al., 1990).

On the whole, the role of external factors in synchronizing the spawning of planktotrophic strategists shedding gametes in water is evident (Ims, 1990).

External synchronizers are probably also involved in the control of spawning of species with lecithotrophic larvae. Thus, simultaneous shedding in lecithotrophic strategist sea stars *Fromia indica* and *F. monilis* and polychaetes and corals comprising reefs was recorded off western Australia (Marsh, 1987).

In temperate latitudes in which species with planktotrophic or lecithotrophic larvae usually exhibit seasonality of reproduction, species with direct development and those brooding the young vary in this respect. Even within the same genus *Lasaea* (family Erycinidae, Bivalvia), there are species which reproduce round the year and others which adhere to a restricted reproductive period (Beauchamp, 1986).

The emergence of larvae of marine invertebrates into the ambient medium may be directly stimulated by external factors but in many species, the cyclicity of environmental variations has been described within the framework of heredity in the form of biological clock and the emergence of larvae proceeds in accordance with these clock even in the absence of external sitmuli (Morgan, 1995).

It is beyond the scope of this book to analyze the breakdown of normal processes of reproduction and development of marine invertebrates under the influence of a wide gamut of anthropogenic environmental factors such as increased metal content in the water, eutrophication followed by red tides, water contamination with petroleum products and others (Myint, Tyler, 1982; Tracey, 1988; Khristoforova, 1989; Malakhov, Medvedeva, 1991; Vashchenko, Zhadan, 1995; Tyurin, Khristoforova, 1995). In the context of reproductive strategy, attention should be drawn to Lawrence's concepts (1990, 1995) regarding different responses to toxic factors in marine invertebrates with different survival strategies based on Grime's (1979) hypothesis about the relationship between survival strategy of plants and their response to stress (reduction of productivity) and demage (reduction of biomass). Nevertheless, the presently available data are not adequate to draw a definite conclusion as to the advantages or otherwise of direct or indirect development of marine organisms under conditions of

anthropogenic contamination and other stress-causing factors (Pechenik, 1999).

Population characteristics and reproductive strategy

A detailed study of the population structure of the species under study is not the objective of this section. I only wish to draw attention to those population features which may be a consequence of planktotrophic or lecithotrophic reproductive strategy.

All planktotrophic, and to a lesser extent lecithotrophic strategists with larvae are characterized by complex life cycles with the population divided as bottom and pelagic or semipopulations (Beklemishev, 1960; Sveshnikov, 1977; Wilbur, 1980). Bottom semipopulations of planktotrophic strategists are usually large in number and biomass and hence are regarded as dominant species in the community. Planktotrophic strategists may exist in diverse habitats, their larvae are transported over long distances, and they successfully settle in diverse substrates. As a result, populations of planktotrophic strategists have large distribution ranges which, in the course of the entire life of a single generation, may spread over several tens or hundreds of km (Scheltema, 1981). The large population number together with significant size of organisms results in a large population biomass. The large population of organisms in turn is the result of combination of high fecundity, multiple reproduction, and long life span. Examples are the settlements of *Crenomytilus grayanus* and *Patiria pectinifera* in Peter the Great Bay. Settlements of each of these species are homogeneous in the genetic context (Pudovkin et al., 1981) and their population number has attained levels of 200 million organisms (Biryulina, 1972a, b).

Stearns (1976) and Schaffer (1974b) made theoretical computations which confirmed the effect of long life span on the comparative stability of population density under conditions of variable recruitment and relatively high level of survival of adults. Long-lived marine invertebrates maintain their population level through successful recruitment which may occur once in many years (Pearson, Muno, 1991; Nakaoka, 1993). Population fluctuations reflect fluctuations in production of gametes, success of larval transport and their mortality (Menge, 1991). The high longevity and iteroparity evolved in an environment of fluctuating mortality of offspring (Orzack, Tuljapurkar, 1989). Sea urchins represent one such species. Thus, in favorable years (with respect to food availability), the concentration of sea urchins *Strongylocentrotus droebachiensis* in the feeding grounds ensures close contact between sexes in the period of insemination while the high fecundity of urchins, as a result of excellent trophic base, makes for a spurt of larval population followed by a steep rise in number of adults (Levitan, 1995; Meidel, Scleibling, 1998). The long life span of planktotrophic startegists is largely explained by their freedom from the pressure of predators. This reduction in predation pressure (and effects of other

unfavorable factors) is a consequence of these organisms attaining a fairly large, safe size, at which they become inaccessible to predators and less subjected to other adverse factors. Thus, the rapid and prolonged growth of organisms during their life period, especially in the prereproductive period, is an important factor in maintaining the population structure of the species with planktotrophic strategy. In the reproductive period, mature organisms in the settlement organize into temporary spawning aggregates, which ensures synchronized shedding of gametes, enhances fertilizability of eggs in organisms with external insemination, and creates reproductive contact during internal insemination (Pennington, 1985; Lawrence, 1987; and others). In some mobile bivalves and echinoderms—planktotrophic strategists—the settlement structure has in it some aggregates of juveniles inhabiting and feeding in the so-called nursery areas, i.e., regions of rearing, which are more favorable for the young than the habitats of adults (Chia, 1984). The young living together with adults come under protection of adults in case of danger (Breen et al., 1985). In sessile forms, irrespective of the presence or absence of planktotrophic larvae, juveniles inhabit together with adults as a consequence of the gregarious settling of larvae (see p. 115).

Goshima (1982) drew attention to the population stability of *Mya japonica* (species with planktotrophic strategy) in spite of unstable recruitment. Population stability is ensured by the long life span of these organisms and repeated reproduction as well as by their distribution characteristics within the habitat. This implies that larvae of species with planktotrophic strategy are transported over long distances and settle satisfactorily on different substrates. Thus, the population is made up of several settlements with diverse habitat conditions. Such a subdivision of the population moderates the action of diverse unfavorable factors which influence randomly one or the other settlements and stabilize the population (Stenseth, 1980; Kreslavskii, 1984). On the whole, species with planktotrophic larvae consist in turn of populations inhabiting under different conditions and population characteristics (Scheltema, 1975; O'Foighil et al., 1984; and others). This promotes a longer, compared to species with lecithotrophic strategy, survival of the species (Scheltema, 1977; Jablonski, Lutz, 1983).

Genetic polymorphism

Levins (1968) developed the concept of adaptive strategies as the aggregate of population characteristics adapted to time and space parameters of the habitat environment. The extent of spatial nonhomogeneity and temporal unpredictability (the latter is not the same as instability, e.g., seasonal changes of environment represent an index of its instability but they are predictable—Ayala, 1981) sensed by organisms is expressed as the grain size of environment. The environment may be sensed by organisms as

coarse- or fine-grained. The aggregate of features of the genetic system, adaptive to environmental parameters, may be called the adaptive genetic strategy (Valentine, 1977). Genetic polymorphism (GP) of proteins detected by the electrophoretic method is a component of the adaptive genetic strategy. When evaluating intraspecific genetic polymorphism, the possibility should be taken into consideration of interspecific hybridization quite widely prevalent in some groups; such hybridization results in the formation of fully competent larvae capable of settling (Beaumont et al., 1993).

The most adequate measure of GP is the average heterozygosity for all the loci investigated. The heterozygosity for a single locus is $1 - x_i^2$, where x_i is the frequency of the ith allele.

According to Valentine (1977), the level of GP is determined primarily by counterbalancing selection. The reproductive volume of the population also influences the level of GP: populations with low reproductive bulk may have a low GP as a result of genetic drift. Having studied the relationship of species and environmental parameteres with the level of GP, Valentine concluded that the distribution range of the species, biological characteristics of reproduction, and stability of the physical environment of habitat are not related to the level of GP; he supported the view of a relationship between level of GP and size of organism and the degree of its mobility and homeostasis (Selander, Kaufman, 1973; Selander, 1977). Turning attention to the distinct relationship between GP and level of diversity of community and hence with level of stability of trophic resources, Valentine explained it in terms of adaptive strategy: in a coarse-grained (on temporal scale) environment, i.e., under unstable trophic conditions, for example in high latitudes species acquire a strategy with a small number of flexible genotypes. In an environment that is fine-grained (on temporal scale), species become specialists with a large number of highly adapted genotypes and high level of GP. Ayala (1981) associated the level of GP similarly with the level of trophic stability and cites examples in favor of direct dependence between these indexes. However, for proof, Ayala compared the GP of species inhabiting under different conditions and pertaining to unrelated groups of organisms. This aspect prompted just criticism by Hedgecock and Nelson (1981).

Grassle (1972) interpreted the relationship between level of GP and species diversity differently; according to him, the level of GP should be high under unpredicatable conditions to ensure adaptation of the species to unpredictable conditions. The diversity of species under such conditions is low since communities should consist of big populations in order to maintain a high level of GP. Under predicatable conditions, according to Grassle, reproductive population volumes are likely to be low and hence the level of GP low. Similar views were expressed by Bretsky and Lorenz (1970) who held that under stable conditions GP decreases, while in an

unstable environment, accumulation of abundance of genotypes occurs and high GP is maintained. Selective importance of genetic polymorphism explains its high level among bivalve *Musculium partineium* (Sphaeriidae) inhabiting temporary biotopes (MacLeod et al., 1981). According to the data of Rodhouse et al. (1986), the heterozygosity for many loci correlates positively with fecundity in *Mytilus edulis*. Heterozygosity also promotes survival of mollusks under conditions of oxygen deficiency (Borsa et al., 1992).

All of the above investigators assume that the GP of proteins has adaptive significance for the organism, is maintained by counterbalancing selection, and represents the material for subsequent evolution as conditions change. It has further been assumed that, at any given moment, there is an adequate level of variability caused by mutations and that natural selection plays the main, constructive role in maintaining GP. However, the adaptability of GP presumes a high level of heterozygosity, higher than actually observed. Instances of allele mutations identified electrophoretically, which are convincingly related to certain conditions of adaptations, comprise only a small proportion of all mutations at the molecular level. Nei (1983) did a detailed review of concepts on the decisive influence of natural selection on the level of GP. Concepts explaining the GP as neutral mutations arose as an alternative to the views of Neo-Darwinists who regarded the GP of proteins as an adaptive phenomenon Kimura and his colleagues have presented these views very lucidly. Selander (1977) cites from Calder (1973, p. 44) as follows:" only a total demolition of the views of Kimura and his colleagues and ardent supporters can preserve intact the Neo-Darwinism of the 1960s. With every passing year, however, such a possibility is increasingly receding". What are the views of Kimura and his supporters? According to them, natural selection (primarily as stabilizing selection which discards extreme variants) determines the phenotypic evolution while molecular evolution is determined primarily by mutations and random genetic drift with random fixation of neutral of near-neutral alleles. Under some conditions, neutral mutants may become the starting material for adaptive evolution (Kimura, 1983).

The behavior of neutral mutation in a population with a definite volume comprises the base for the quantitative neutral theory of GP. Fixation of a new allele in a population requires time equal to $4/N_e$ generations from the moment of its onset. If it is assumed that each mutation is unique and leads to the manifestation of a new allele, the anticipated frequency of heterozygotes $H_e = \frac{4Ne \cdot V}{4Ne \cdot V + 1}$, where V is the rate of neutral mutation per generation and N_e the effective reproductive volume of the species.

The rate of mutations can be calculated from the rate of replacement of amino acids in protein which is quite constant in the course of evolution.

The average rate of manifestation of new mutations is 1×10^{-7} mutations per locus per annum. Knowing the generation time, the value of V can be calculated. N_e can be substituted by N when the upper limit of anticipated heterozygosity is obtained. If the neutral theory holds, the observed heterozygosity will be equal to or less than the theoretical value. Data on heterozygosity show that in spite of the ideas of supporters of the selectivity theory about excessively high genetic variability (so high as to be neutral), the variability in fact is very low compared to the level anticipated under neutral mutations, i.e., there are factors which reduce the level of GP, especially a small effective reproductive volume of the species at present or in the past ("bottleneck" effect).

From the viewpoint of the neutral theory, Hedgecock and Nelson (1981) also studied other factors that might reduce GP. Among them are: normalizing selection which eliminates the weak, unfavorable mutations; inequal ratio of sexes; and inequal contribution of parent organisms to recruitment of the next generation. The last factor may be significant for species with planktotrophic larvae. The significant dispersal of a number of gametes per adult organism which recruit the next generation, may reduce the effective reproductive strength by a few orders, especially under conditions of correlated survival of sibs (Hedgecock, Nelson, 1981). In this context, Hedgecock and Nelson draw attention to the patchiness of the plankton medium. In our view, the patchiness of the substrate for settling is more important for survival.

Thus, from the neutralistic viewpoint, reproductive strategy and genetic polymorphism are related through the reproductive volume of the species. The reproductive strategy aimed at enhancing brood care ensures stable reproduction of population and relatively constant, albeit low, reproductive volume of the species. Among species with planktotrophic strategy, the population (possibly, the species as a whole) may attain very high values exceeding the corresponding levels for species with lecithotrophic strategy. Further, the reproductive volume of the species too attains high values. Under unfavorable conditions, absence of brood care, absence of complex mechanisms of ensuring the contact of gametes, and other factors, may result in a sharp drop in reproductive volume. Thus, among species with planktotrophic strategy which have survived the "bottleneck" effect in the reproductive population, values of heterozygosity may be less than in species with lecithotrophic strategy.

Data are given below on mean heterozygosity (Manchenko, 1986) and nature of development for 17 species of sea stars. The average value of heterozygosity in stars with lecithotrophic strategy (six species) is 0.175 and in stars with planktotrophic strategy (11 species) 0.129. Thus, there is a growing tendency toward heterozygosity among sea stars on transition to lecithotrophic strategy. Similar results were recorded for gastropod mollusks (Berger, 1973; Ward, Warwick, 1980, from Cameron, 1986).

Among species leading a sessile life style in a highly congested environment, fluctuation of reproductive volume of the species are less manifest than among mobile forms. Bivalves shipworms may serve as an example of such a group. Population-genetic data recorded by Hoagland and Turner for 32 loci covering six species of shipworms showed that the level of heterozygosity was highest among species with planktotrophic strategy; the level was average for species with larvae delayed in the maternal organism and lowest in species with prolonged brooding (Hoagland, Turner, 1981). Hoagland and Turner explained the very low heterozygosity among *Teredo bartschi* as the effect of the parent organism (introduced population of this species was studied). The average value of H for six species was 0.084 or 0.100 without *T. bartschi* (the average heterozygosity for marine invertebrates H=0.147). Hoagland later confirmed these data and related the high heterozygosity of planktotrophic species to their high fecundity and stable strength of the population (Hoagland, 1986). Thus, the pattern observed for shipworms is the converse of that in sea stars. From the viewpoint of the neutral theory of polymorphism, the very high level of heterozygosity among planktotrophic *Bankia gouldi* and *B. fimbriatula* can be explained by the high reproductive volume of these species; further, population fluctuations that are natural for species with planktotrophic strategy do not result (due to the very high density of settlements) in catastrophically low values of reproductive volume as occurs among mobile forms. The low level of genetic polymorphism among larviparous oysters compared to the high value in oysters with external insemination, can also be similarly explained (Buroker, 1985).

Transition to asexual reproduction in some species of echinoderms sharply modifies population genetic structure since the division of adults results in formation of a multiplicity of genotypic copies adapted to local conditions. Electrophoretic analysis of asexual populations of sea star *Coscinasterias calamaria* revealed low genetic diversity and considerable shift from the genetic equilibrium state, which is confirmed by the clonal structure of these populations (Johnson, Threlfall, 1987).

Habitats and reproductive strategy

Distribution patterns of different types of reproductive strategy among marine benthic invertebrates generally correspond to the patterns of quantitative distribution of animal benthos in the World Ocean. In turn, the quantitative distribution of animal life on the floor of seas and oceans represents a somewhat blurred projection (Belyaev, 1977) of the distribution of plants (Vozzhinskaya, 1977), plankton (Semina, 1977) and primary production in general (Koblents-Mishke, 1977). The distribution of all forms of life in the ocean conforms to a latitudinal and circumcontinental zonality. The former is determined by planetary variations of various abiotic factors

in the meridional direction. The latter is determined by the effect of coasts on the characteristics of water circulation and accumulation of biogenic elements (Vinogradov, 1977). Thus, the distribution of various types of reproductive strategy is characterized by latitudinal and circumcontinental zonality.

Latitudinal zonality is manifest in reduction of the proportion of species with planktotrophic strategy on transition from the tropics to higher latitudes. Planktotrophic strategy is replaced by lecithotrophic; further, direct development or viviparity predominates in the latter at higher latitudes. According to older data in the shelf of the tropical zone of oceans, species with pelagic larvae comprise 90-95% of the total number of species (Thorson, 1946, 1950). Among bivalves inhabiting the European coast from Gibraltar to Denmark, species with lecithotrophic strategy comprise only about 30% of the number of species with planktotrophic strategy and, moving northward, the proportion of the former increases; at Spitsbergen, it exceeds the proportion of the latter by 1.5 times (Ockelmann, 1965a, b). According to our calculations, planktotrophic larvae are characteristic of only one-fifth of the species of sea stars studied in the Arctic and boreal zones. In the tropical and subtropical zones, the proportion of such stars exceeds 50%. In Antarctic and subantarctic regions, species with planktotrophic strategy are rare (Kasyanov, 1987a).

Circumcontinental zonality is manifest in reduction in proportion of species with planktotrophic strategy as depth of habitat of the species increases. Thus, in the region of Skagerrak, the proportion of these species among the total number of species of bivalves at depths up to 40 m exceeds 80% while at depths greater than 400 m it is less than 20%. At Spitsbergen, such species constitute about 20% at depths up to 40 m and are replaced totally at depth 100 m by species with lecithotrophic strategy (Ockelmann, 1965). We noticed a similar tendency among sea stars in oceans in general. Planktotrophic reproductive strategy was observed in roughly one-half of the species studied in the world literature at depths up to 400m but only every fourth or fifth species inhabiting regularly at depths exceeding 400 m has planktotrophic larvae (Kasyanov, 1987a). Like latitudinal, circumcontinental zonality is not absolute in character and there is no total replacement of development with pelagic larvae in bathyal or abyssal regions (Tyler et al., 1982; Tyler, Gage, 1984).

It should be remembered, however, that development with lecithotrophic larva or direct development is common among some groups and, under favorable conditions is found more often than development with planktotrophic larva. Examples are sea cucucmbers, brittle stars and partly sea stars. In these groups, on transition to high latitudes and at increasing depth, further replacement of planktotrophic by lecithotrophic strategists is seen.

Thorson (1936, 1950) relates the noticed patterns of distribution of

developmental types with the quantum of heat and level and stability of trophic resources for larvae. In the coastal zones of tropical and temperate waters, the level of phytoplankton production is adequate for the development of planktotrophic larvae; in polar waters, trophic resources are unstable and larvae do not succeed in undergoing complete development in the period of brief spurts of phytoplankton growth under low temperature conditions: in areas far away from the coast, the level of output of phytoplankton is low at great depths and is inadequate for ensuring growth of planktotrophic larvae. It is of the same importance to ensure trophic resources to adult, parent organisms to which Thorson (1936) has also referred. If productivity is high, for example in the shelf zone of temperate waters, many species occupying different trophic levels and different positions in the communities have adequate resources for massive production of gametes while maintaining planktotrophic strategy. If productivity is low, for example in the shelf zone of the Arctic, only a few species that are dominant in the community receive adequate resources for maintaining planktotrophic strategy. For other species, such a strategy is inaccessible and they take to lecithotrophic strategy. Finally, in regions with poor productivity—abyssal and Central Arctic basin—planktotrophic strategy is totally or almost totally replaced by lecithotrophic strategy.

In this context, let us recall Valentine's hypothesis about the predominant death of species with planktotrophic strategy at the border of the Permian and Triassic epochs. Acccording to him, the structure of the Early Triassic communities was similar to the present subarctic communities with seasonal or irregular variations of productivity characteristic of the subarctic. This led to a reduction in proportion of species with planktotrophic larvae compared to the corresponding level in the warmer Permian period (Valentine, 1986).

In a detailed review on larval ecology, Jablonski and Lutz (1983) presented data on gastropod mollusks which contradict Thorson's conclusions about the increased proportion of mollusks with pelagic larvae in the tropics compared to temperate latitudes. The high proportion of non-pelagic development in some regions of low latitudes has been explained by Clark and Goetzfried (1978) as due to the trophic stability of these regions. This weakens the pressure of selection on the high capability for dispersal and thus promotes more energy-efficient nonpelagic development.

The patterns of latitudinal distribution of developmental types can be studied from the viewpoint of the stochastic model of evolution of strategies of the life cycle (Jablonski, Lutz, 1983). According to this model, severe conditions of surface waters at high latitudes which cause a high and inconstant level of larval mortality, promote evolution toward organisms with late maturation, low reproductive effort, and low fecundity.

With no pretension to a review of the reproductive biology of bivalves and echinoderms in different oceans of the world, I am nevertheless attempting a brief review of recent reports which have analyzed the reproduction and development of groups under investigation in shallow regions and at high latitudes, at great depths, and in specific regions of deepwater thermal sources.

Low latitudes

In many tropical species, reproduction proceeds all through the year including the relatively cold winter season during which some fall in reproductive activity is observed. Such data were obtained for bivalves (Braley, 1982; Toral-Barza, Gomes, 1985; Vales Rojas, 1985), sea cucumbers (Harriot, 1980, from Conand, 1982), brittle stars (Mladenov, 1983), and sea urchins (Moore et al., 1963; Cameron, 1986a, b). According to our data, during winter-spring period of the 50 species of bivalves inhabiting the shallow waters of South Vietnam, gonads of 70% were in the prespawning or spawning state. Of the 50 species of echinoderms, 50% were in such a state (Kasyanov et al., 1989). This provides indirect proof for the conclusions of the above-cited investigators. At the same time, judging from our data (Kasyanov et al., 1989), some species in winter have reduced gonads with an insignificant content of immature gametes. Data on the annual gonadal cycles with a limited reproductive period can be found in the literature for tropical species. Such is the case, for example, with the reproduction of bivalve mollusk *Asaphus deflorata* in the Bahamas (Berg, Alatalo, 1985), sea cucumbers *Actinopyga echinites, Holothuria nobilis, H. fuscagalva,* and *Thelenota ananas* in New Caledonia (Conand, 1981, 1982), sea star *Acanthaster planci* on Guam (Birkeland, 1982), brittle star *Ophiothrix oerstedi* (Mladenov, 1983), sea urchin *Stomopneustes variolaris* in Madras region (Pearse, 1969b), *Mellita quinquesperforata* in Florida (Lane, Lawrence, 1979), *Echinometra viridis* and *E. lucunter* in Puerto Rico (Cameron, 1986b). The seasonality of reproduction has also been demonstrated for other tropical species of sea urchins (Yakovlev, 1989; Laegdgaard et al., 1991). Sea cucumbers with lecithotrophic development *Phyrella fragilis* and *Afrocucumis africana* inhabiting the littoral waters of southern Taiwan reproduce only in the early spring as temperature rises (Chao et al., 1993). It is well known that sea cucumbers of the order Dendrochirota with lecithotrophic larvae inhabiting temperate waters also have a reproductive season restricted to a few warm months (McEuen, 1988; McEuen, Chia, 1991). Evidently, tropical fauna, more than that of temperate waters, is characterized by the coexistence of extremely divergent variants of reproductive activity of constituent species. This may be associated with the divergent combinations of abiotic and biotic factors which influence the successful reproduction in each species.

High latitudes

Among the general features common to the reproductive biology of Arctic and Antarctic benthic invertebrates are the high proportion of species manifesting brood care (Thorson, 1936, 1950; Mileikovsky, 1971). It may be pointed out, however, that many of the common and widely distributed species are not of the brooding type but bear lecithotrophic or even exotrophic larva (Pearse, Bosch, 1986; Bosch et al., 1987a). Scallop *Adamussium colbecki*, gigantic by Antarctic standards, inhabiting in particular oligotrophic habitats, produce pelagic exotrophic larvae. Larval feeding is probably ensured by spurts of organic matter and bacteria (Berkman et al., 1991). According to Mileikovsky (1973a, 1977), although the proportion of species with pelagic larva decreases sharply in high latitudes (Thorson's law), this type of development does not vanish completely; species which pursue development with planktotrophic larvae have high population numbers in the communities. Examples here are bivalve *Hiatella arctica* inhabiting the Greenland coast (Thorson, 1936) and gastropod mollusk *Nacella concina* (Picken, 1980; Picken, Allan, 1983), and sea star *Odontaster validus* (Bosch et al., 1987b) inhabiting the Antarctic. This highly common and prominent Antarctic sea star is characterized by large accumulation of nutrients compared to other sea stars inhabiting there in the pyloric appendages, which readily ensures gametogenesis (McClintock et al., 1988; McClintock, 1989) extending for more than 12 months and concluding with synchronized releases of gametes; significant variations in gonadal processes and larval density have been observed in different years (Stenwell-Smith, Clarke, 1998).

Many species of bivalve mollusks inhabiting the Antarctic bear offspring in the mantle cavity or in gills until metamorphosis or release lecithotrophic larvae contained in envelopes with a short planktonic or demersal phase (Pearse et al., 1987, 1990). It has recently become clear that in the Antarctic (at least in the Weddell Sea), the proportion of bivalve mollusks with planktonic larvae is considerably more than assumed before- at two-thirds of the total number of species, one-half of which (14 species) produce planktotrophic larvae (Hain, Arnaud, 1992).

Larval development in the polar waters proceeds very slowly—up to 3-40 weeks (Strathmann, 1978b; Pearse, Bosch, 1986). Among actively feeding larvae, planktotrophy is sometimes replaced by bacteriotrophy (Rivkin et al., 1986). The presence of planktotrophic larvae in the plankton of polar waters is associated with the summer spurt of phytoplankton (Clarke, 1979).

Gonadal processes in mollusks and echinoderms proceed slowly in polar waters and the gametogenic cycle may extend for 1.5-2 years (Pearse, 1965; Pearse, Giese, 1966; Boivin et al., 1986; but: Yakovlev, 1983). In sea urchin *Sterechinus neumayeri* inhabiting Antarctic shallow waters in McMurdo

regions, 96% of the entire output goes into production of germ cells, in sharp contrast to the expense of germ cell production in temperate-water and subtropical sea urchins in which it does not exceed 40% (Brey et al., 1995). Population recruitment in *Sterechinus neumayeri*, in spite of colossal expenses in reproduction, is very little; much of the gonadal production in the form of long-lived pelagic larvae of this sea urchin (about four months) is eaten by planktonic organisms, thus creating an extremely powerful relationship between bottom and pelagic constituents of the food chain of the Antarctic community (Brey et al., 1995).

Like *Sterechinus neumayeri*, another Antarctic sea urchin, *S. antarcticus*, dominating in the Weddell Sea communities at depths of 450-1,200 m similarly produces small-sized eggs (250 μm) and exotrophic larva. Reproduction is seasonal (Brey, 1991) but only 48% of available energy goes into germ cells. This species is typical of K-strategists with slow and prolonged growth, with maximum somatic production in 14-20 years and maximum production of germ cells in 42-51 years. Another K-strategist inhabiting the coastal waters of Kerguelen Island in the subantarctic, sea urchin *Abatus cordatus*, grows slowly in the first two years; its reproduction is independent of season and development proceeds without larvae, by brooding (Mesphoulhe, David, 1992).

The reproductive biology of bivalves and echinoderms inhabiting the Arctic or Antarctic has several differences due to the diverse history of formation of fauna of these regions as well as the differences in conditions of habitats, which are very severe in Antarctic waters. Most of the Antarctic bottom invertebrates are characterized by low fecundity, large egg diameter, brooding or viviparity, slow development, delayed maturation, and slow gametogenic processes (Clarke, 1979; Duchene, 1985). In some groups of echinoderms, e.g., sea urchins, brooding species are found only in the southern polar latitudes. It has been assumed that the evolution of brooding in the Antarctic sea urchins proceeded in a background of decreasing primary production in Antarctic waters in the periods of main glaciations (Poulen, Feral, 1996). Among Antarctic (not Arctic) species, sea urchin *Abatus nimrodi* and sea star *Notasterias armata* are "champions" in egg size. The gigantic egg sizes in these groups are explained not by the large energy consumption for development, but by the need for raising young of large size (Lawrence et al., 1984; McClintock, Pearse 1986). Selection toward large-size juveniles leads to loss of planktotrophic larvae (Strathmann, 1977, 1978c); a precondition for this is the accumulation of not carbohydrates but lipids as nutrient reserve in eggs of high latitude organisms (Kaufman, 1976). Lawrence (1987) has cited various examples of brooding among antarctic echinoderms including development of embryos in the maternal ovary.

Islands and Underwater Mountains in Open Sea

Oceanic islands of volcanic origin are set off from the shelf zone by ocean basins and settlement of coastal waters of islands is only by larval transport or rafting (Paulay, 1994). A few species cross the barrier of open sea.

Unlike significant endemism of terrestrial biota of islands, marine organisms inhabiting the coastal waters of islands and slopes of underwater mountains are characterized by a low level of endemism (Scheltema, 1986, 1989, 1995). Thus, only 8% of malacofauna of Ascension Island in the central tropical Atlantic represent endemic species, the rest (92%) being continental in origin (Rosewater, 1975; Scheltema, 1995). Only 2% of gastropods of shallow waters scouring the ocean Pitcairn Island are endemic (Paulau, 1989).

Species with an extensive distribution range quite often covering both sides of the ocean and with planktotrophic (in many families, teleplanic) larvae inhabit the coastal waters of islands. Plankton data confirm the hypothesis concerning the significant role of larvae in the contemporary distribution of many sublittoral invertebrates on central Pacific islands (Scheltema, 1989). At the same time, local populations of ocean islands are not pseudopopulations maintained only by larval inflow but full-fledged reproducing populations. Reproduction of a local population is possible because the mass of larvae produced by these populations is held by local currents and, drifting in them, larvae develop to the stage of settling and metamorphosis, returning at the end of the pelagic period to a site suitable for settlement (Schultz, Cowen, 1994; Scheltema et al., 1996).

A correlation for genetic distance between island and mainland populations has been demonstrated for sea star *Acanthaster planci* in Okinawa, Saipan, Guam, Fiji, Townsville, and La Paz with geographic distance between these regions. Planktotrophic larvae of this species are responsible for the extent of interpopulation gene flow (Nishida, Lucas, 1988).

The role of teleplanic larvae in settlements in coastal waters of oceanic islands is beyond doubt (Palumbi et al., 1997; Lessios et al., 1998) but many species in these waters have direct development. Such species can originate in the waters of islands with ships, through rafting or as a result of evolution of species formerly having larvae (Helmuth et al., 1994; Ingolfsson, 1995). For example, analysis of mitochondrial DNA of brooding bivalve mollusks of *Lasaea* spp. in the North Atlantic showed close genetic similarity between island and continental populations not linked by contemporary surface currents; it has been suggested that colonization of islands proceeded as a result of ship movement and rafting (O' Foighill, Jozefowicz, 1999).

Deepwater regions

For deepwater species, a slow tempo of life cycles caused by food inadequacy is a characteristic feature (Young et al., 1994). In them, metabolism as well as fecundity are usually low and their body size is small. According to Smith (1994), deepwater species exhibit the highest degree of K-strategy of life cycle.

Settlement on soft and hard substrates in deepwater regions proceeds considerably more slowly than in the sublittoral region; communities are long represented only by juvenile forms and thus larval inflow (usually lecithotrophic, short-lived larvae) and conditions promoting their settlement determine the fate of these communities (Smith, Hessler, 1987; Mullineaux, 1988; Mullineaux, Butman, 1990).

Reports published in the last three decades have greatly enriched our concept on reproduction among deepwater organisms. According to Sanders (1979), both r- and K-strategists prevail in deepwater regions but the latter are more common. From the viewpoint of reproduction, K-strategists are characterized by low fecundity and absence of reproductive seasonality. Species with seasonal reproduction are usually sessile or show restricted movements and are not common (Rokop, 1974). In 1979, Bouchet and Waren (1979) provided data for the first time on the presence of planktotrophic larvae among deepwater mollusks following a study of the larval shell of deepwater gastropod mollusks which is well preserved in adults. Later, these data were confirmed by isotope analysis of the material of larval and definitive shell which revealed differences in the temperature conditions of habitats of larvae and adult organisms (Bouchet, Fontes, 1981). Scheltema (1994) expressed doubt about the conclusions of Bouchet and Waren (1979) and Bouchet and Fontes (1981) on the prevalence of vertical migration of larvae of deepwater gastropod mollusks upward into the photic zone. According to Scheltema, it is possible that the actively feeding larvae of deepwater gastropods do not abandon the deep zones but feed in the bottom layer on heterotrophic organisms—bacteria, flagellates, influsoria, or even suspended or dissolved organic matter.

Bivalves. Poor access to food for bivalves at great depth leads to reduction in growth and fecundity while feeding efficiency improves (Oliver, 1969). The fecundity of deepwater bivalve mollusks varies from 2 to 30,000 eggs. Only two oocytes mature at one time in protobranchia of genus *Microgloma* (Scheltema, 1994). An increase in life span and high reproductive success with an increase in egg size compensates for the drop in fecundity. Species of Protobranchia, Septibranchia and family Thyasiridae, characterized by small size and long life span comprise 95% of deepwater bivalves. Thus, *Tindaria callistiformis* inhabiting at a depth of 3,500 m survives for 150 years and attains a length of 6-8 mm; its gonads do not develop for 30-40 years and reproduction sets in at about 100 years of age. Hermaphroditism,

although common for deepwater bivalves, is not obligate. Some species develop directly while others have drifting larvae; brooding species have not been detected (Allen, 1979). Among deepwater bivalve mollusks from the bathyal and abyssal Atlantic Ocean, only 6-7% have planktotrophic or, more accurately, actively feeding larvae (Knudsen, 1979; Scheltema, 1994).

Echinoderms. Information is available on the seasonality or reproduction in deepwater regions with apparently constant habitat conditions. In particular, seasonality of reproduction has been noticed in deepwater sea urchins *Echinus acutis* and *E. elegans* on the Scottish continental shelf (Gage et al., 1986), in deepwater sea star *Dytaster grandis* (Tyler et al., 1990), and in spatangoid sea urchin *Brissopsis lyrifera* at a depth of 1,000 m in the Mediterranean Sea (Ferrand et al., 1988). British researchers have made important contributions to understanding the reproductive biology of deepwater echinoderms. Following a study of reproduction, development, and recruitment among 14 species of sea stars, 10 species of sea urchins, 4 species of brittle stars, and 3 species of sea cucumbers in deepwater (1,000-2,900 m) communities in the northeastern Atlantic, this group of researchers detected diverse reproductive cycles and cytological processes comprising them (Harvey, Gage, 1984; Gage, Tyler, 1985; Tyler et al., 1987; see also p. 77). More importantly, Tyler and his colleagues identified diverse variants of development—with planktotrophic larvae, with lecithotrophic larva, and direct development; species with lecithotrophic larva and direct development dominate at these depths. The presence of planktotrophic reproductive strategy in deepwater regions which calls for considerable synchronism of reproduction, compels consideration of external synchronizers of reproduction. Since physical conditions in this deepwater region are constant, these researchers assumed that factors controlling reproduction are the seasonal inflow of organic matter descending from the surface (Tyler et al., 1982, 1984). Seasonality of reproduction is seen in general among few species; most species of lecithotrophic strategists reproduce round the year (Tyler, 1986). Seasonality of reproduction processes in deepwater invertebrates has been associated in recent years with seasonality of movements of organic matter, "sea snow", falling after a spurt of reproduction of planktonic microalgae from the ocean surface to its floor. According to Eckelbarger and Walting (1995), bottom invertebrates from different phyletic branches respond to this "snow" differently: either with the commencement of gametogenesis and rapid shedding of gametes thereafter, or spawning with release of planktotrophic larvae, or commencement and synchronization of gametogenesis with postponing spawning due to the prolonged period of vitellogenesis. As a result, synchronized gametogenesis occurs in some deepwater species while this is not so in others. In some species of sea stars, sea urchins, and brittle stars from the deepwater regions of the northeastern Atlantic, vitellogenesis

follows the flow of organic matter to the bottom (Tyler, 1988; Gage, Tyler, 1991; Campos-Creasey et al., 1994). For deepwater echinoderms with distinct seasonal reproduction, small-diameter eggs and planktotrophic larvae are common; the absence of seasonality of reproduction correlates with large egg diameter and lecithotrophic development (Tyler, Young, 1992).

"Sea snow" exerts little influence on the dynamics and intensity of gametogenesis and the emergence of larvae of predators, parasites, or species that receive energy and sustenance from chemoautotrophic symbionts or in the form of dissolved organic matter, compared to its influence on detritophagous species (Scheltema, 1994).

Deepwater organisms with their sparse density are particularly sensitive to the unreliable recruitment caused by great death and drift of larvae and hence in cases of planktotrophic strategy, deepwater organisms such as sea urchin *Echinus affinis* are characterized by a life span longer than that of organisms inhabiting lesser depths (Gage, Tyler, 1985).

American researchers working in submersibles obtained interesting results. Judging from the diameter of mature oocytes and egg cells, of the 19 species of deepwater sea stars, sea urchins, and cucumbers, 15 species have planktotrophic larvae. Larval cultures of deepwater sea urchins *Aspidodiadema jacobi* and *Stylocidaris lineata* showed that larvae of the former take to active feeding in the pluteus stage while larvae of the latter do so in the prism stage. Growth tolerance to a wide temperature range helps these larvae pass successfully through the various water layers and rise to the surface (Young, Cameron, 1987). Compared to larvae of sea urchins inhabiting shallow waters, larvae of deepwater sea urchin *Aspidodiadema jacobi* have new larval structures facilitating their prolonged swimming and feeding (George, Young, 1995).

Regions of deepwater thermal vents

The attention of biologists was recently drawn to the most interesting finds of American researchers in the regions of deepwater thermal vents in Galapagos Rift and the Eastern Pacific Rise (see: Turner, 1981; Jones, 1985; Nesis, 1987). Fortunately, the first group of researchers included biologists who studied reproduction and development of marine invertebrates. Therefore, investigations were planned in submersibles so as to obtain data on the development and reproductive biology of species comprising the communities, primarily bivalve mollusks.

Along with unique sources of food and energy, specific species composition and considerable distances between settlements, hydrothermal communities are characterized by high density and biomass of most of their constituent species and high growth rate of individual organisms (Turner and Lutz, 1984). Lutz (1988) draws attention to the ability for rapid

settlement and rapid growth as properties characteristic of species inhabiting deep thermal springs.

The find of settlements of the same species around hydrothermal springs lying considerably apart suggests larval transport by flume cones from the spring regions followed by lateral spread for hundreds of meters on the floor surface (Mullineaux et al., 1991). Larvae of bivalve mollusk *Calyptogena* sp., endemic for deep thermal springs, were found only in cones (Kim, et al., 1994; Mullineaux et al., 1995). According to these investigators, larval dispersal is a key phenomenon for hydrothermal species since some thermal springs may survive for only a few years.

Species with planktotrophic larva and species with lecithotrophic development are found among bivalves inhabiting hydrothermal vents in the region of Galapagos Rift and in the region of sulfide seepages on the west coast of Florida. Bottom currents in these regions (velocity 18-33 cm^{-1}) may transport demersal larvae for distances of 100-1,000 km over a few weeks or months, thus providing a link between isolated pockets of such communities (Lutz et al., 1980; Turner, 1981; Lutz et al., 1984; Turner et al., 1985).

Calyptogena magnifica (family Vesicomyidae) living in hydrothermal communities of Galapagos Rift is a gonochoristic species which produces a large number of yolk-rich eggs that develop without planktotrophic larvae (Turner et al., 1985). It is quite possible that chemoautotrophic bacteria serve as an additional source of energy for growth of *C. magnifica* (Alatalo et al., 1984). This species possesses high reproductive potential thanks to its early maturation, long life span, and high fecundity. Asynchronous gametogenesis occurs in gonads of *C. magnifica* and the spawning season is weakly manifest. Mytilid *Bathymodiolus thermophilis* cohabiting with *C. magnifica* is characterized by protandry and females are larger in size than males. *B. thermophilis* produces numerous small eggs from which exotrophic larvae develop and are capable of spreading for hundreds of km along underwater mountain ranges and negotiating the space separating the thermal springs. According to genetic data, a settlement obtains about eight migrants during its life cycle (Craddock et al., 1995). Analyzing these and other facts, Berg (1985) concluded that the reproductive strategies among bivalve and gastropod mollusks inhabiting deepwater thermal communities are quite diverse. Rex (Rex et al., 1979) likewise concluded that isolating the reproductive strategy associated with deepwater hydrothermal vents is no more meaningful than forming a common deepwater species or a common littoral reproductive strategy.

Many new facts on reproduction and development of the inhabitants of this amazing world have come to light in recent years as a result of using well-conceived new techniques during expeditions in the region of deep hydrothermal vents (Young, Eckelbarger, 1994). It has been confirmed that there is no single reproductive strategy among its inhabitants and the

reproductive strategy characteristic of a given phyletic branch is usually the same in shallow-water species as well as in species of regions of deep thermal springs (Gustafson, Lutz, 1994). On comparing species of bivalve mollusks from these vents and those from the usual deepwater regions, it can be said, however, that the proportion of species with continuous or multiple reproduction in the annual cycle in the regions of thermal springs is high, due to the relative abundance of material resources and energy (Gustafson, Lutz, 1994).

CONCLUSIONS

Without using the specific term "reproductive strategy", investigators in the field of development and reproduction of marine invertebrates have nevertheless recognized that the presence of planktotrophic or lecithotrophic larva involves a set of characteristics which combine to form adaptation complexes.

Ivanov's (1937) views about adjustment of ontogenesis for the larva or adult organism can be regarded as a thoretical premise of morphological approaches to classifying reproductive startegies. These views were further advanced by Svetlov (1972) who emphasized that adjustment for the larvae implies the triggering (at a given stage) of ontogenesis of a part of the hereditary system which ensures larval development. Dondua (1983) analyzed three types of ontogenesis in organisms which differ in stages controlled by the maternal genome (before commencement of cleavage, up to the stage of blastula and up to the stage of gastrula or larva formation) and related these variants to adjustment of development for larva or adult organism. Control of gene activity at the level of gene batteries and spatial control of gene activity in adjoining cells, depending on the cell's position in the cell system, characterize the initial type of embryogenesis with larval development (Davidson, 1991; Davidson et al., 1995, but see Lacalli, 1997). Larval cells possess these two systems of gene control.

Unlike larval cells, imaginal cells "standing aloof" from morphogenic processes occurring during larval formation, along with the above gene control systems, possess a new system of spatial local control. This system includes independent gene activity in imaginal cells separately at each population of imaginal cells and through the products of gene activity, control the entire development of the organism. Manifestation of new local systems of gene control in evolution generates new morphological space, a new morphological field, ensuring explosive manifestation of new life forms in the history of the Earth as it occurred in the Cambrian (Cameron et al., 1998; Peterson et al., 1997).

The local system of gene control includes in particular the *Hox* gene clusters, which are not used in the embryonic and larval stages of development of contemporary species with indirect development, but function in the course of metamorphosis when the structural plan of the adult organism is formed from the imaginal primordia. This has been

confirmed by the data of expression of this gene in the development of sea urchin *Strongylocentrotus purpuratus* (Cameron, 1998). *Hox* genes codify the transcription factors and serve as molecular markers of cell position along the main body axis (McGinnis, Krumlaut, 1992; Akam, 1998). Another gene, *Brachyury*, investigated in the development of sea urchins is seen even in larvae in the line of secondary mesenchymal cells initially on the vegetative plate of the mesenchymal blastula, later at the tip of the archenteron, and finally in the secondary mesenchymal cells (Harada et al., 1995). This gene is responsible for formation of the notochord in the development of Deuterostomata (Satoh, 1998).

Thus, the course of development into larva or direct development is predetermined by the presence and system of control of the activity of the respective genes. A comparative study of genomes in animals with different reproductive strategies has only recently commenced (Jeffery, Swalla, 1992; Swalla et al., 1993; Strathmann, Eernisse, 1994; O'Foighill, Smith, 1994; Smith et al., 1995; Hart et al., 1997). Along with homeotic genes controlling the spatial development patterns, analysis of heterochronism genes, i.e., temporal analogues of homeotic genes, is important in the context of reproductive strategy (Slack, Rivkin, 1998).

There is also a veiw of early development as a process not subjected to evolutional changes, all the more so since all the later hierarchical developmental stages depend on the much earlier ones. However, in our view, it would be more rational to consider the entire development as a process comprising different blocks, responding differently to selection pressure (Raff et al., 1991a, b). Thus, during direct development of sea urchin *Heliocidaris erythrogramma*, larval stages are not only eliminated but even altered compared to the original earlier development—micromeres forming in predecessors the larval skeleton are not formed but hydrocoel is formed even in the gastrula stage (Raff et al., 1991b). Not a few such examples are known.

It is clear that increase in egg size per se does not suffice for modifying the type of development (Wray, Raff, 1991). Transition to direct development is not a simple loss of program of larval development but a comprehensive rearrangement of all morphogenic processes of embryonic and larval development (Emlet, 1990; McMillan et al., 1991; Wray, Raff, 1991; Raff, 1992). Transition to a new developmental program may occur rapidly on the geological scale—in sea urchins the transition to direct development took place roughly in eight million years (Raff et al., 1991b). There have been not less than 14 such transitions in this class (Emlet, 1990).

In the preceding pages, we attempted to demonstrate the dependence of ontogenetic processes leading to formation of planktotrophic larva on events arising in the reproductive system of the organism. An attempt has been made to show the relationship between morphological aspects of reproduction and development and ecological and population aspects. It

would be advantageous to study the entire picture of such diverse characteristics within the framework of concepts on reproductive strategy. The concept of larval and embryonic reproductive stategies has been formulated and characteristics of planktotrophic larval reproductive strategy as applied to marine bivalves and echinoderms described in detail. Planktotrophic strategy has been compared with the lecithotrophic (see Table 1). Approaches adopted in this work for a thorough description of reproductive biology may be useful for analyzing the reproductive biology of other groups of organisms. Concepts on exotrophic and endotrophic and especially planktotrophy and lecithotrophic reproductive strategies incorporated in this book, can be applied to various groups of organisms although the range of related characteristics and their trend may vary in different groups.

Table 1

Comparative characteristics of planktotrophic and lecithotrophic reproductive strategies in marine bivalves and echinoderms

Characteristic	Planktotrophic strategy	Lecithotrophic strategy
Characteristics of Individual Organisms		
Features Describing Ontogenesis as a whole		
Brood care	Not characteristic	Characteristic
Material and energy consumption on brood as a whole	Relatively high	Relatively low
Material and energy consumption for producing one individual	Relatively low	Relatively high
Fecundity	High	Low
Larval presence	Essential	Possible
Active larval feeding	Essential	Absent
Pelagic period	Relatively prolonged	Relatively short or absent
Metamorphosis	Essential	Possible
Size of juveniles	Relatively small	Relatively large

Contd...

Table 1 contd...

Characteristic	Planktotrophic strategy	Lecithotrophic strategy
Size of organisms on attaining maturation, irrespective of juvenile sexuality	Relatively large	Relatively small
Dependence of reproduction and development on external factors	Relatively high	Relatively low
Features Describing Sex Formation		
Early gonadal formation	Possible	Characteristic
Gonochoristic determination of sex	Characteristic	Not characteristic
Single sex change	Possible	Not characteristic
Repeated sex change	Not characteristic	Characteristic
Functional hermaphroditism	Absent	Possible
Protandry	Possible	Characteristic
Protogyny	Absent	Possible
Sexual dimorphism	Weakly manifest	Could be well manifest
Male dwarfism	Absent	Possible
Features Describing Gonadal Activity and Reproduction		
Number of gonial divisions	Relatively more	Relatively few
Duration of vitellogenesis	Relatively short	Relatively long
Multiple nucleoli in oocyte	Absent	Possible
Resorption of growing oocytes in gonad	Possible	Characteristic
Features Describing Gametes		
Egg size	Relatively small	Relatively large
Amount of yolk in egg	Relatively small	Relatively more
Amount of lipids in egg	Relatively small	Relatively more
Egg envelopes	Poorly developed	Well developed
Size of spermatozoon head	Relatively small	Can be large
Atypical spermia	Absent	Possible

Contd...

Table 1 Contd...

Characteristic	Planktotrophic strategy	Lecithotrophic strategy
Characteristics of Populations and Species		
Size of population	Large	Small, large ones possible
Agewise distribution	Unstable	Stable
Sex ratio	Equal	Perhaps unequal
Mortality of larval cohorts	High	Low
Mortality of settled juveniles	High	Low
Stability of recruitment	Low	Relatively high
Population increment	Rapid rise possible	Relatively slow
Ability to settle in new regions and new habitats	High	Low
Size of distribution range of species	Relatively large	Relatively small
Gene flow between population	Relatively large	Relatively small

Although Table 1 does not exhaust all the characteristics distinguishing the two types of strategies of bivalves and echinoderms, it serves as an "intermediate point" on the way to understanding the entire set of features constituting these strategies. Finally, planktotrophic and lecithotrophic strategies are not distinctly demarcated except in some extreme types in which they can be regarded as alternates. Analysis of correlations of characteristics which are of value for reproduction helps in a quantitative description of the area of overlap or the extent of deviation between reproductive strategies of different types (see Buroker, 1985). The game theory approach for analyzing reproduction and development of organisms is yet a weak link but its extensive coverage of problems under study is anticipated. It would then possibly help in prediction of the course of evolution of reproduction strategies and reconstruction of rescue of offspring by ancient species in the ecological theatre of antiquity.

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